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ON AN EARLY TERTIARY LAND-CONNECTION BETWEEN NORTH AND SOUTH AMERICA

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THAT the two great continents—North and South America—have only become joined to one another by land in later Tertiary times, is a widely accepted assumption. Yet the various authorities who have made this problem a subject of special investigation have not all come to precisely the same conclusions as to the geological age during which this union of the two continents was brought about.

A study of the marine fishes on both sides of the isthmus of Central America, for example, convinced Dr. Günther[1] that up to a recent geological period the latter was only represented by a chain of islands similar to that of the Antilles. But the number of species of fishes on the Atlantic and Pacific coasts of Central America that were supposed to be identical has been considerably reduced during more recent surveys. They no longer amount to more than 4.3 per cent. of the total number of fishes known to occur in both areas. Professor Jordan[2] on that account maintains that the isthmus has not been depressed during the lifetime of most of the existing species. The submergence, he argues, must have supervened at a more remote time. In the belief that the

[1] Günther, A. C. L. G., "Study of Fishes," p. 280.

[2] Jordan, D. S., "Study of Fishes," Vol. I, pp. 274–280.

Miocene may be taken as the date of origin of the modern genera of marine fishes, he contends that an open communication between the two oceans may have existed during that geological period. It is important to note that the sea currents seem at that time to have set westward, thus favoring the transfer of Atlantic rather than Pacific types across the isthmian area.

Mr. Regan[3] is inclined to put the date still a little further back in urging that the marine connection between the two oceans ceased to exist at the beginning of the Miocene.

An investigation of the Crustacea and their distribution led Dr. Ortmann[4] to the conclusion that at the dawn of the Tertiary era an oceanic connection was in actual existence between the Atlantic and the Pacific in the isthmian region. This communication, he thinks, persisted until the Miocene. In the commencement of that period the isthmus was elevated, thus joining North and South America.

The Mexican amphibians and reptiles have been utilized by Dr. Gadow[5] in the solution of the same interesting problem with the result that he assumes the establishment of land-continuity between North and South America in either late Oligocene or early Miocene times.

The whole character of neotropical zoology, remarks Dr. Wallace,[6] whether as regards its deficiencies or its specialties, points to a long continuance of isolation of South America from the rest of the world, with a very few distant periods of union with the northern continent.

Geologists have discussed this subject mostly from paleontological evidence. Professor Gregory[7] clearly demonstrated that the idea of an interoceanic connection as late as the Pleistocene period, as suggested by Dr. Spencer,[7a] could no longer be entertained. In arriving

[3] Regan, C. T., "Fishes of Central America," p. xxx.

[4] Ortmann, A. E., "Geographical Distribution of Decapods," p. 359.

[5] Gadow, H., "Mexican Amphibians and Reptiles," p. 236.

[6] Wallace, A. R., "Distribution of Animals," Vol. II, p. 80.

[7] Gregory, J. W., "Palæontology of the West Indies," p. 305.

[7a] Spencer, J. W., "Reconstruction of an Antillean Continent," p. 134.

at a final decision as to the approximate date of orgin of the Central American land bridge, he was mainly influenced by Professor Scott's reference to the occurrence of Caryoderma a supposed glyptodont edentate in the Miocene Loup-Fork deposits. He urged, therefore, that the waterway across Central America was in all likelihood finally closed in the lower Miocene or possibly even in the upper Oligocene. As Caryoderma, however, is now believed to be a reptile and not an edentate, this argument no longer holds good.

Less definite are the results obtained by Dr. Hill[8] after a careful study of the rocks near the Isthmus of Panama. The only geological periods, he thinks, since the Mesozoic era, during which the Pacific and Atlantic Oceans could have been in communication with one another, would be the Eocene or Oligocene. It is important to note that Dr. Hill's conclusions were based entirely on his observations at the Isthmus of Panama. The geology of the remainder of Central America is as yet too imperfectly known to form the basis for similar speculations.

The most important pronouncement perhaps which has yet been made on the subject under discussion is that by Professor Osborn.[9] His intimate knowledge of the fossil terrestrial mammals of North America enabled him to affirm that North and South America were joined to one another more than once, as Wallace had suggested. The first union occurred in Mid-Cretaceous and perhaps early Tertiary times. Hereafter the continents separated once more until the Pliocene period.

Dr. Smith Woodward,[10] Mr. Lydekker and also Professor Depéret[11] hold similar views with regard to the more recent junction of the two continents.

The evidence on which Professor Osborn based his belief in the first and much earlier land connection between North and South America was unknown when Mr. Lydek-

[8] Hill, R. T., "Geological History of the Isthmus of Panama," p. 269.

[9] Osborn, H. F., "Mammalian Palæontology," p. 99.

[10] Woodward, A. S., "Palæontology," p. 429.

[11] Depéret, C., "Transformations of the Animal World," p. 282.

ker[12] wrote his work on the Geographical History of Mammals. He was under the impression, therefore, that the mammalian fauna of the South American region had been totally isolated from that of North America up to about the end of the Miocene. I shall shortly return to Professor Osborn's views as soon as I have completed my brief historical review of the first problem.

Professor Lapparent[13] concurs with Mr. Lydekker's opinion that the interchange of waters between the Atlantic and Pacific oceans across Central America could only have ceased to exist at quite the end of the Miocene period.

Finally, in his treatise on the development of continents, Dr. Arldt[14] maintains that the Central American land bridge must have originated at the commencement of the Pliocene period, and with this view I fully agree. Part of Central America no doubt had already risen above the ocean at a much earlier period, but in its present outlines and extent it must be regarded as a geologically recent development.

All those in fact who have seriously considered the problem, either from the standpoint of a marine or a terrestrial zoologist or from that of a paleontologist concur in the opinion that North and South America were separated from one another by a marine channel or by wide seas during part of the Teritary era. This, however, is the only point in which there is a general agreement. While some contend that the junction between the two continents had only been effected in comparatively recent geological times, others hold that within the life history of the great class of mammals, either in the early Tertiary or late in the Secondary era, a land bridge between North and South America had once before existed, by means of which an interchange of the faunas could have been brought about. It is this supposed earlier land connec-

[12] Lydekker, R., "Geographical History of Mammals," p. 119.

[13] Lapparent, A. de, "Traité de Géologie," p. 1318.

[14] Arldt, Th., "Entwicklung der Kontinente," p. 597.

tion and its probable nature and extent that I wish to discuss.

Dr. Wallace already vaguely indicated that there may have been several very distant periods of union in the past of the Southern with the Northern continent. This supposition received a startling confirmation by the discovery first by Dr. Wortmann and then by Professor Osborn[15] of true armadillo remains in the middle Eocene beds of Wyoming. If he does not actually speak of a direct land connection between the two continents in early Tertiary times, Professor Osborn[16] suggests as much in his remark that this discovery "adds another fact to the growing evidence that North and South America were related in the Mid-Cretaceous and perhaps early Tertiary and then separated again until the Pliocene." He does not specify in any way in what manner this relationship had been brought about. His views would be of particular interest, considering that Dr. von Ihering's extensive zoological and botanical researches have led him to believe that the South American continent itself must be of comparatively recent geological origin.

The latter declares that South America had arisen as a continent only since the Oligocene period. It then consisted of two parts united by a narrow strip of land in the west, which later on developed into the great mountain chain of the Andes. These two parts, which he calls "Archiplata" and "Archiguiana," were previously separated from one another. The first embraced Chile, Argentina, Uruguay and southern Brazil, the other the highland of Venezuela and Guiana. Each of these possessed, according to Dr. von Ihering,[17] its own characteristic fauna and flora and these were totally distinct from one another.

A somewhat similar theory as to the origin of South America, largely based on the geographical distribution of fresh-water decapods, has been advanced by Dr. Ort-

[15] Osborn, H. F., "An Armadillo from the Middle Eocene," pp. 163–165.
[16] Osborn, H. F., "Mammalian Palæontology," p. 99.
[17] Ihering, H. von, "Archhelenis and Archinotis," p. 79.

mann.[18] In place of the present Southern continent he thinks that toward the end of Mesozoic times, there existed the old Brazilian land (Archiplata), an Antillean continent (including the West Indies and Venezuela) and also the Chilean coast range. These three land masses were separated from one another by wide oceans. Just before the close of the Secondary era the Antillean continent, and with it Venezuela and even the Galapagos Islands, became united with western North America, the latter being then still detached from eastern North America. When Venezuela in early Tertiary times at last became fused with the other larger South American land masses, the interoceanic connection across Central America had severed it from North America.

Under such geographical conditions the Wyoming edentates alluded to by Professor Osborn could only have been derived from Venezuela, it being the sole portion of the present Southern continent that had any relationship with North America in those remote times. No fact, however, has been brought to light, either in the recent or fossil history of the edentates to lead us to imagine that they had originated in the northern part of South America.

That South America owes its origin to the union of several independent land masses is so clearly indicated by the existing fauna of the continent, that a similar evidence should also be revealed by a study of its rocks and fossils.

The geology of South America is unfortunately as yet little known. Yet even such a cautious observer as Professor Suess[19] ventured to suggest, on stratigraphical grounds, that an arm of the sea may have penetrated right across the continent in Cretaceous times. The archaic rocks of eastern Brazil and Guiana certainly were then raised above the sea, since the younger formations appear to be superimposed with great regularity further and further to the west of this ancient formation. Dr.

[18] Ortmann, A. E., "Geographical Distribution of Decapods," pp. 365–366.

[19] Suess, E., "Antlitz der Erde," Vol. II, p. 683.

Katzer[20] contends that during part of the Mesozoic era the Pacific ocean extended eastward to the shores of this land, whose rivers then drained westward into the ocean, as they even continued to do until Miocene times.

While it is therefore by no means evident from the geologist's point of view how and when the various land masses became joined to form the present South America, the geographical distribution of the living fauna, together with a study of the paleontology, has furnished most valuable hints as to the probable geological history of the continent.

Dr. Gill claims that the fishes are among the best indicators of former geographical conditions. Turning to the most recent studies on the South American fish fauna, those of Professor Eigenmann,[21] we find that he also is impressed by the dissimilar elements of which it is composed. He explains this varied character of the fauna by the supposition that two independent land masses, originally separated in the region of the Amazon valley, became welded together in early Tertiary times.

In his attempted restoration of the geographical conditions of South America during the Eocene period, Professor de Lapparent[22] depicts an aspect contrasting with that of other observers, and yet he recognizes a division of South America into two parts, for he represents the continent as being dissevered by a marine channel between the Rio Negro in Argentina and Southern Peru.

Of all the maps illustrating ancient distribution of land and water, that of Dr. Arldt[23] is the most striking in originality. He connects northern South America in late Cretaceous times by land with western Mexico, but not by way of Central America. He assumes that the latter was submerged at that time and that an independent land bridge extended from southwestern North America through the Galapagos Islands to Colombia. This north-

[20] Katzer, F., "Geologie des Amazonengebietes," p. 254.

[21] Eigenmann, C. H., "Fishes of South and Middle America," p. 528.

[22] Lapparent, A. de, "Traité de Géologie," p. 1455.

[23] Arldt, Th., "Entwicklung der Kontinente" (map 19).

ern complex of land was isolated from the southern part of South America by a wide sea channel stretching right across the continent.

His conception of an extensive land having once flourished to the west of Central America, while the latter was largely submerged, is not altogether new. In alluding to the east-westward trend of the Antillean Cordillera and its abrupt termination on the Pacific coast of Guatemala, Professor Suess[24] makes a suggestion as to its former westward prolongation. Precisely at the point, he says, where the arcuate continuation of this chain might be expected to meet the principal chains of South America, lie the volcanic Galapagos Islands.

Various indications in the structure of the Isthmus of Panama moreover left the impression on Dr. Hill's[25] mind that large areas now covered by the Pacific, to the west of the isthmus, were once replaced by an extensive land surface.

Nothing more, however, can be deduced from geological testimony as to the presence of any land connecting North and South America at a time when Central America may have been still wholly or partially submerged. Nor can we even surmise from these suggestions at what geological period such hypothetical land may have existed. Other methods will have to be employed in order to discover the manner by which the Eocene armadillos reached North America.

If we examine the whole eastern Pacific coast line from Alaska to Cape Horn, we notice that there are two areas that have apparently remained entirely unsubmerged since Jurassic times to the present day. One of these occupies part of western Mexico and Lower California, the other a strip of the southern coast line of Chile. It is the latter coast cordillera which Dr. Burckhardt[26] believed to be the remaining remnant of a mighty Pacific continent, because porphyritic conglomerates of Cretaceous age are heaped

[24] Suess, E., "Antlitz der Erde," Vol. II, p. 263.
[25] Hill, R. T., "Geology of the Isthmus of Panama," p. 217.
[26] Burckhardt, C., "Traces géologiques d'un continent," pp. 12–14.

against its eastern flank, whereas still further east the latter grade into fine-grained rocks, thus indicating that the land from which they were derived lay westward, out in the ocean.

While we need not here dwell upon the theory of a former Pacific continent[27] so ably supported by Professor Haug on purely geological grounds and by Professor Hutton on zoogeographical data, I should like to draw attention to some features in the geographical distribution of animals and plants which prove that southwestern North America and southwestern South America are intimately related to one another in their fauna and flora. This relationship can not be explained as the product of a similarity in soil and climatic conditions. It is not a case of mere convergence. It can be shown that it already existed in the distant past, and I venture to think that this relationship implies the presence of a former direct land connection between these two ancient areas, when the continent of South America was still in the making.

It was Dr. Wallace[28] who first directed attention to the remarkable fact that many genera of insects from the north temperate regions reappeared in temperate South America, being generally absent in the intermediate stations. He explained this phenomenon by the supposition that the northern forms had traveled southward during successive glacial epochs when the mountain range of the Isthmus of Panama might have become adapted for their advance in that direction. Their southward passage was believed to have been facilitated by storms and hurricanes which carried the insects across unsuitable territories.

This interpretation of a striking feature of geographical distribution seems to have been considered satisfactory at the time. At any rate no one has raised any protest so far as I am aware. Yet I am not at all disposed to admit its correctness.

[27] More detailed information on the theories relating to an ancient Pacific continent will be published in my work on the geological history of the American fauna.

[28] Wallace, A. R., "Distribution of Animals," Vol. II, pp. 45–47.

Let us take, for example, the case of Carabus, a genus of running beetles so familiar to North American entomologists. They are by no means easily transported to great distances by gales and hurricanes as Dr. Wallace avers, for the simple reason that these beetles can not fly. Their wing cases are permanently soldered together, and being generally found under clods of earth or beneath stones, the action of winds can have no appreciable influence on their dispersion. They are typical inhabitants of the northern hemisphere, being abundant in Europe, northern Asia and North America. A single species occurs in western Mexico. No Carabus has ever been taken in Central America or in the northern or middle states of South America. Yet in Chile and spreading into Argentina, no less than eleven species have been observed. For a distance of about fifty degrees of latitude the running beetles of the genus Carabus are quite absent and then reappear further south in numbers. Those entomologists, like Mr. Born,[29] who have made a special study of the Carabidæ, consider them eminently fitted for the purpose of demonstrating former changes of land and water.

Of the northern genera of butterflies Colias, Lycæna and Argynnis, which occur in Chile, the presumption, at any rate is admissible that they might have been transported to these far distant southern latitudes by accidental or occasional means of dispersal, such as those suggested by Dr. Wallace. Yet the case of the ant Lasius, a northern genus, which reappears in Chile, is more difficult of explanation on such an hypothesis.

We can not say of any of these invertebrates that they are confined to western Mexico in North America, though this appears to be the most southerly point on the northern continent where they occur. On the other hand the primitive earthworm Kerria is only known from Lower California and from the southern part of South America in Chile and Argentina. From the latter country it seems to have spread into Paraguay and southern Brazil.

[29] Born, Paul, "Zoogeographisch-Carabologische Studien."

Of particular importance is the ancient genus of land molluscs Bulimulus. It is quite peculiar to America. Its nearest relation appears to be the Melanesian Placostylus. Bulimulus, which is almost characteristic of the west coast of America, is now divided into three great groups, one of which has its headquarters in Chile and Peru, the second is met with on the Galapagos Islands, Central America and the West Indies, the third is confined to Lower California and Mexico. These three groups are very similar in appearance, but Dr. Pilsbry[30] maintains that this resemblance, which is particularly noticeable between the Mexican and Chilean forms, is not so much a proof of close relationship as the result of similar environment. At any rate we notice here three distinct and discontinuous centers of radiation, two of which are situated on very ancient land surfaces, while the third mostly occupies islands whose origin certainly dates back to early Tertiary times.

Probably a still more ancient invertebrate is the curious Peripatus, an archaic arthropod with an extremely discontinuous distribution. Three distinct groups inhabit America. One of these is confined to southern Chile, another seems to have spread northward along the Andes from a Chilean center as far as Ecuador. At a distance of twenty degrees of latitude north of this northern outpost it reappears in western Mexico, while in Central America lives a third and perfectly distinct group which has spread thence to the West Indies and eastern South America.

In its three distinct centers of distribution all along the west coast of America it bears a certain resemblance to the range of Bulimulus just alluded to. The range is certainly suggestive of a very ancient and more direct communication than obtains at present between western Mexico and Chile.

The flora of the new world retains far more pronounced traces of that curious relationship between the southwestern areas of its two continents. The plants of both Chile

[30] Pilsbry, H. A., "Manual of Conchology," Vol. X, p. 127.

and southwestern North America, moreover, are better known than are the animals. Whatever may be the cause, not only is there a resemblance between families and genera in the two areas; the general similarity of the landscape and especially the occurrence in both of a profusion of cactuses strikes the casual observer at once. Many specimens of northern plants recur in identical forms in those distant regions of South America.

Professor Asa Gray[31] and Sir Joseph Hooker long ago directed attention to this very remarkable phenomenon.

More recently, Professor Engler[32] and Professor Bray have emphasized this affinity and speculated on the problems connected with it. The flora of the Rocky Mountains including the Sierra Nevada Mountains above the transition zone, and the mountains far to the south of them, though separated from one another by a stretch of some ten degrees of latitude of moist tropical country, abound in northern genera of plants such as Ranunculus, Anemone, Geranium, Spiræa, Geum, Rubus, Saxifraga, Vaccinium, Gentiana, Hieracium and others. The greater number of forms occurring in the southern continent are endemic, pointing to long-continued isolation. Yet certain species, even of the Rocky Mountain Arctic alpine region, reappear in the extra-tropical Andes towards the southern extremity of South America, being, so far as is known, wholly absent from the Mexican mountains as well as the tropical Andes. Among these Professor Bray mentions particularly *Gentiana prostrata, Trisetum subspicatum, Primula farinosa* and its variety *magellanica, Draba incana, Alopecurus alpinus, Saxifraga cespitosa, Polemonium microcanthum* and *Collomia gracilis.*

The lower Sonoran elements of plant life are likewise represented in the extreme south. *Oxytheca dendroidea, Chorizanthe commissuralis* and *Lastarriœa chilensis,* for example, do not occur in the vast regions that separate

[31] Gray, A., and J. Hooker, "Vegetation d. Rocky Mountain Gebietes," p. 292.

[32] Engler, A., "Entwicklungsgeschichte d. Florengebietes," Vol. II, p. 256.

the two areas. A few of these plants may possibly have been casually introduced from the one to the other. But Professor Bray[33] expresses the opinion that in most cases we have to deal with forms which were connected by a remote ancestry, and which flourished at a time and under conditions which permitted a more general distribution.

What these conditions were like he does not venture to inform us, but it must be evident that this flora is much older than the Pleistocene, during which time it has been supposed that the climatic conditions may have favored a southerly advance of northern forms. Specific changes, among certain plants as well as among some animals, seem to proceed with extreme slowness. We have the example of the still living redwood tree (*Sequoia sempervirens*) which has persisted unchanged since Mesozoic times, for the fossil *Sequoia Langsdorfi* is now considered identical with the modern form.

It appears to me possible, therefore, that the well-known and extremely discontinuous range of some of the alpine plants may be interpreted by the assumption that, like Sequoia, they are of vast antiquity and that they have spread along a continuous mountain chain which once extended in a direct line from southwestern North America to western Chile, before the Andes had risen from the floor of the ocean.

We know that a similar relationship between North America and southern South America prevailed already in Mid-Cretaceous times. No less than seventy-five per cent. of the plant remains recently discovered in a Mid-Cretaceous plant-bearing layer in Argentina are characteristic types of the Dakota-group flora.

Commenting on this discovery, Mr. Berry[34] dwells on the remarkable agreement of this southern flora with that developed in Mid-Cretaceous times in western North America. He urges that it certainly points to a community of origin. In these ancient South American deposits all the familiar northern genera Liriodendron,

[33] Bray, W. L., "Relations of the North American Flora," pp. 709–716.

[34] Berry, E. W., "Mid-Cretaceous Geography," p. 510.

Liquidambar, Cinnamomum and Sassafras are met with. Even Platanus, Populus, Quercus and others are represented. No wonder that Mr. Berry[34] came to the conclusion that a geographical connection must have existed between North and South America during Mid-Cretaceous times. He thought that the plants referred to had spread southward from the north, while Professor Osborn favors the view that his Eocene Armadillo had advanced from the south.

Before concluding this short review on the evidences pointing to an early Tertiary direct land bridge between the southwestern portions of North and South America, a few observations on the paleontology of Patagonia and Chile may somewhat elucidate this interesting problem.

Edentates occur in the oldest Tertiary deposits of Patagonia or even pre-Tertiary, if Dr. Florentino Ameghino[35] is correct in assigning a Mesozoic age to the latter. The position which this savant has taken up and so courageously defended has been almost universally assailed. Professor Ameghino still holds that the now famous fossiliferous strata of Santa Cruz, which have yielded such a surprisingly rich harvest of mammalian remains are of Eocene age, while the likewise terrestrial Notostylops beds belong to the Cretaceous series.

The great majority of geologists, on the other hand, are of opinion that the Santa Cruzian deposits belong to the Miocene and the Notostylops beds to the Eocene period.

These beds are separated by marine strata which have been carefully investigated by the members of the Princeton Expedition to Patagonia. The invertebrates collected were described by Dr. Ortmann,[36] who considered them as certainly of Miocene age. He thus concurs in the opinion arrived at independently by the many eminent paleontologists, that both the terrestrial deposits above alluded to, the Notostylops and Santa Cruzian beds, are of Tertiary age.

[35] Ameghino, Flo., "Formations sédimentaires de Patagonie."

[36] Ortmann, A. E., "Princeton Expedition," p. 288.

To all appearances the question was finally settled when Dr. von Ihering[37] again challenged the results obtained by Dr. Ortmann, pointing out certain discrepancies in his determinations. Dr. von Ihering now maintains that only 4.9 per cent. of the species from the Santa Cruz marine beds are still living and, as the formation moreover corresponds to those of Oamaru in New Zealand and of eastern Australia, now generally included in the Eocene, he feels no hesitation in placing the Patagonian marine beds in the latter series. He, therefore, entirely supports Dr. Fl. Ameghino's latest views as to the Eocene age of these strata.

If Dr. von Ihering's conclusions are substantiated, and his arguments appear to me convincing, the more recent terrestrial Santa Cruzian deposit must be either of Oligocene, or as Dr. Ameghino believes, of Upper Eocene age.

Let us for a moment consider the geographical conditions in early Tertiary times of that region of South America in which these beds are found. The similarity in character of the Patagonian marine fauna on the east coast with the Tertiary of northern Chile on the west coast of the continent implies the existence of a connection between the two oceans. This supposition is further strengthened by the fact that eight per cent. of the eastern or Patagonian species of marine mollusca are found in the western Tertiary beds of Navidad in Chile.

Since a number of northern types of molluscs make their appearance in the upper divisions of the Patagonian beds, Dr. von Ihering suggests that the supposed old land connection between Brazil and Africa had at that time been ruptured, thus opening a way for an invasion of the northern fauna. I have not previously alluded to this land bridge, Ihering's southern Atlantis or Archhelenis, because I am not dealing with this problem at present. It is not necessary, however, to conclude from the presence of northern molluscs in the upper Patagonian marine beds that this supposed land bridge had broken down

[37] Ihering, H. von, "Mollusques fossiles de l'Argentine," p. 95.

completely in upper Eocene times. They could just as well have come from the Pacific, which seems to have freely communicated with the Atlantic across Patagonia. Not only are these northern invaders present in the Chilean deposits on the Pacific coast, there are many genera in the latter according to Dr. von Ihering,[38] such as Conus, Purpura, Oliva, Cassis, Cypræa and Littorina which never penetrated as far east as Patagonia at all. They thus denote the manner of dispersal of all the northern forms from north to south, and it appears as if they had gradually crept southward along some ancient coast line. But since there is no reason to suppose that the present Pacific coast of South America had come into existence already in early Tertiary times, we may assume that the ancient coast line lay farther west.

Down to Miocene times the influence of the Caribbean and even the European marine fauna continued to be felt on the Pacific side of South America. Dr. Ortmann[39] tells us that the north Peruvian Miocene fauna shows close affinities with the faunas alluded to. Several observers remarked on the circumstance that when Central America was submerged in early Tertiary times, the Caribbean and Atlantic species generally seemed to be drawn towards the Pacific by a strong current. We have noticed that the effects of this current in carrying northern Atlantic forms are traceable in the Tertiary deposits all along the Pacific coast of South America as far south as northern Chile and even on the Atlantic side of the continent in Patagonia, which then freely communicated by a marine channel with the Pacific.

On the other hand, the Tertiary molluscs of Chile and California are very distinct from one another. This apparently implies that a barrier was interposed between the northern coasts of California or rather between the main portion of the Pacific coast line of North America and that of South America. Hence it tends to support my argument, that western Mexico and part of lower

[38] Ihering, H. von, "Mollusques fossiles de l'Argentine," p. 514.

[39] Ortmann, A. E., "Tertiary Invertebrates of Santa Cruz," p. 320.

California had a direct land connection with Chile. Dr. von Ihering[40] suggests that the Antillean arc which is continued to Guatemala and there abruptly terminates on the Pacific coast may have been continued westward in early Tertiary times in a great peninsula comprising the Galapagos and Sandwich Islands. He applied the term "Pacila" to it.

My reason for preferring to connect western Mexico and Chile in the manner I conceived, rather than adopt Dr. von Ihering's proposal, is that the spreading of Caribbean and Atlantic shallow water forms of molluscs indicates a continuous shore line running north and south.

The Pacific coast of South America as it appears today had not yet emerged in early Tertiary times. The Andes were only just beginning to make their appearance. They must have risen as a series of islands parallel to the ancient coast that lay out in the west.

I picture to myself southern Chile as forming the extreme apex of a long penisula extending southward from western Mexico. Sometime during the Eocene period it became disconnected from Patagonia. The long peninsula was subsequently more and more reduced in size until only high mountains, such as the volcanic cones of the Galapagos Islands, remained above water. The peculiar lizards belonging to the genera Amblyrhynchus and Conolophus inhabiting these islands have their nearest relation in Phymaturus, which is confined to Chile, and not as we might expect to the much less distant Peru, Ecuador or Colombia. As long as any parts of the peninsula remained above water and attached to Mexico, it may have added its mammalian fauna to that of North America.

In such a manner it may possibly have come to pass that the northern genus of porcupine Erethizon is, according to Professor Scott, more like the fossil Steiromys from the Santa Cruz beds than the latter is to any of the South American porcupines. Steiromys, as Professor

[40] Ihering, H. von, "Archhelenis und Archinotis," p. 318.

Scott[41] informs us, is only a little more primitive than Erethizon, the change from the one to the other involving but a slight modification.

Erethizon is unknown in North America from pre-Pleistocene deposits, but there is no reason to assume that it had not originated long before the Pleistocene period. South American types of mammals may have existed in western North America from early Tertiary times onward without having left their remains in the more ancient deposits.

The theory of the former existence of a great lobe of land connecting western North America with southern South America during the beginning of the Tertiary era, while Central America and northern South America were still largely submerged is sustained by many facts in the geographical distribution of plants and animals. It seems to me to explain the undoubted affinities prevailing in the two areas in a better manner than by any other hypothesis. Against it may be urged that it is an unwarranted supposition to assume that existing species of plants can have preserved their specific characters since the Eocene period. Still we must not forget that one plant at least, *Sequoia sempervirens,* has lived without any appreciable change down to the present time from those remote ages. And even if we altogether eliminate the testimony elicited from a botanical source, there still remain zoological factors of importance as buttresses of the hypothetical bridge I have constructed.

May, 1909.

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NOTES ON THE RELATIONS OF THE MOLLUSCAN FAUNA OF THE PERUVIAN ZOOLOGICAL PROVINCE

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HAVING recently summarized the faunal relations existing between the mollusca of the deep sea, off the western coast of South America, and those of other regions,[1] it has happened that in reporting on a collection of mollusca submitted for examination by the government of Peru, it fell to me to compile a census of the mollusca inhabiting the shallow waters and coasts of the region known as the Peruvian zoological province. Such an enumeration had not been made for something like half a century. The much fuller knowledge of these animals now possessed by scientific students makes the number of species belonging to this region much greater than was formerly supposed, and modifies in consequence the conclusions formerly arrived at.

The littoral fauna has practically nothing in common with that of the abysses. The relations of the two groups of animals to each other, to adjacent faunas, and to the Tertiary fauna, have recently assumed a special interest, from the discussions by von Ihering and others as to the routes of Tertiary migrations.

It was thought therefore that a summary of the results deduced from a study of this faunal list would have a certain general interest not only for malacologists but for the students of historical geology.

The littoral marine molluscan faunas of the west coast of the two Americas, excluding the Arctic and Antarctic faunas properly so-called, were recognized more than

[1] *Bull. Mus. Comp. Zool.*, XLIII, No. 6, pp. 207–211, 1908.

half a century ago in their main outlines by Woodward.[2] They comprise, beginning at the north:

1. *The Oregonian Province,* extending from the limit of floating ice in Bering Sea south to Point Conception, Cal.

2. *The Californian Province,* ranging from Point Conception south to Lower California.

3. *The Panamic Province,* from Lower California including the Gulf of California, south to the Bay of Guayaquil, Ecuador.

4. *The Peruvian Province,* extending from Guayaquil south to the vicinity of the island of Chiloë in southern Chile.

5. *The Magellanic Province,* from Chiloë to the Fuegian Archipelago, and for a short but undetermined distance north on the Argentine coast, on the Atlantic side.

These provinces will eventually be recognized as containing minor divisions, with which, on this occasion, we are not concerned.

The distribution recognized in the term province appears to be directly dependent on the temperature of the surface stratum of the sea, which, in its turn, is distributed by ocean currents. In the case of the Peruvian Province a branch of the eastward-flowing South Pacific current diverges from the main stream and impinges upon the coast of South America in the vicinity of Chiloë Island. Thence it follows the coast northward, until by the northwesterly trend of the Peruvian shores it is diverted, in the vicinity of Point Aguja and Cape Blanco, to the westward, where it continues in the direction of the Galapagos group of islands. This current, known as the Peruvian or Humboldt current, throughout its entire extent maintains a temperature (varying with the season) of from 65° to 70° Fahrenheit. The temperature of the surface off Aguja Point, Peru, in November, was 65° F. The temperature of the water in the Magellanic Province in mid-summer varies from 50° F. in the straits themselves, to 55 °F. on the Chilean coast in the vicinity of Valdivia.

[2] "Man. of the Mollusca," pp. 373–377, 1856.

The surface temperatures of the Peruvian current, as related to those of the Magellanic water, are therefore warmer; and, as compared with the Panamic waters, markedly colder. Precisely such a relation to the coast of North America is held by the southerly branch of the North Pacific current, which reaches the coast near Sitka with a summer temperature of 65° to 68°. This has diminished in the latitude of San Francisco Bay to 54 °F., but the current continues until in the vicinity of Point Conception, California, it is diverted off shore in a manner entirely analogous to the fate of the Peruvian current at Point Aguja.

The water of the Panamic Province is less disturbed by currents, receives the full heat of the tropical sun, and, as shown by Professor Alexander Agassiz, emerges from the Gulf of Panama, follows the coast toward Cape San Lorenzo, and is there diverted off shore toward the Galapagos Islands. Trees from the mainland with leaves still adhering to them are occasionally cast upon the shores of the Galapagos, as observed by Professor Agassiz; showing clearly that the current is not only present but has no inconsiderable motion. The temperature of this water near the coast of Ecuador and only a few miles from the limit of the Peruvian current, in November, varied from 70° to 83° F., and in March and April from 78° to 85° F. Among the Galapagos Islands the range in April was 81° to 83° F.

It will be noticed therefore that the currents fully account for the peculiarities of the Galapagos mollusk-fauna, which exhibits large contributions from the Panamic and Peruvian faunas with only a very unimportant tincture of the Indo Pacific in its make-up.

A series of surface temperatures measured in November at right angles to the Peruvian current off Point Aguja, by the U. S. S. *Albatross,* began with a temperature of 65° F. close in shore, rose quickly to 69° and later to 70° in the middle of the current, and declined again to 69° F. on its western edge.

The first exploration of the molluscan fauna of the Peruvian Province which was systematically carried on, was that of Hugh Cuming. He was resident for some years at Valparaiso, later dredged and collected vigorously at various points of the Bay of Guayaquil. Tradition has handed down the account that a severe earthquake (referred to by Darwin in the Voyage of the *Beagle*) laid bare a long stretch of coast where the shore mollusks, elevated above their natural situs, were accessible to the collector by the thousand. Mr. Cuming collected largely, and on his return to England these collections gave an opportunity to the systematic naturalists to describe many new Peruvian and Chilian shells. This lasted for a good many years. Broderip, Sowerby, Swainson, Gaskoin, Powys, Deshayes and Reeve worked on these collections during the first half of the nineteenth century. According to Woodward[3] Mr. Cuming's collection embraced 222 species from the coast of Peru, south of Paita, and 172 species from the coast then politically included in Chile. Of these probably half were common to the northern and southern portions of the province. A little later the explorations of Humboldt and Bonpland added a few species; the majority of their collection, it would seem, was not worked up.

M. Alcide D'Orbigny's South American investigations seem to have been, so far as this province is concerned, largely restricted to the Chilean portion of it. He collected 160 species, one half of which were common to Chile and Peru, while only one species was common to Callao and Paita. The inference naturally drawn from this last fact by Woodward and others was that the northern border of the province lay between those two ports. But this conclusion was due to imperfect knowledge, and is completely refuted by later information. At present more than 200 species are known to be common to Paita and Callao.

D'Orbigny's report with its atlas of fine illustrations

[3] Manual, p. 376.

is a classic source for information, relating, however, to South America as a whole rather than to the Peruvian Province.

Collections made by Gay and others, worked up in his monographic Historia de Chile, by Hupé, form the third large and well-illustrated contribution to the malacology of the province, chiefly restricted of course to the southern or Chilean portion.

The last important contributor to a knowledge of this fauna in these earlier days was the German naturalist Philippi, who added numerous species and useful illustrations in the *Zeitschrift für Malakozoölogie*, his "Abbildungen," and his "Atacama Reise."

Of course many minor contributors to the work, such as Lesson, Jonas, etc., might be mentioned, but I propose in this hasty sketch to touch only on the most important. The list of Tschudi's collection, ostensibly from Peru, as described by Troschel unfortunately contains numerous exotic Indo Pacific and Panamic species, so that its authority is seriously impaired. More recently the researches of Ludwig Plate, the Princess of Bavaria and others, have added essentially to our knowledge.

In considering the distribution of species along the coast of the province it should not be forgotten that the collections have not been made with equal thoroughness on different parts of the coast. The ports of Guayaquil, Paita, Callao and Valparaiso have naturally been much more thoroughly explored than any of the rest, and the careful collecting which would obtain the smaller species is not recorded to have been done at all, anywhere.

Dredging also is practicable with difficulty, except in the sheltered harbors which occur so rarely on this coast, or by the aid of a large steamer which could be had only under Government auspices on account of the great expense involved.

The small lots of material derived from the mud which came up on the anchor of the *Albatross* at one or two points, show that proper exploration will certainly reveal

the presence of many small species new or extralimital which are at present unknown. In determining what species should be included in the list I have depended somewhat upon the known characteristics, as regards distribution, of the groups to which the species belong. For instance, if I found a species reported from Guayaquil and belonging to a widely distributed group such as the Pholadidæ, though not actually reported from a Peruvian locality, I have not hesitated to include it, knowing that in all probability it will be found on more thorough search in Peruvian territory. There can be little doubt that a large number of the more mobile of the Panamic species reaching the Bay of Guayaquil will be found to have extended their range more or less within the northern border of the Peruvian Province; just as a certain number of the characteristic Magellanic species have traveled beyond their strict limits and mingle with the southern members of the Peruvian fauna. Species properly belonging to the Panamic Province and not reported as far south as Guayaquil or the Galapagos Islands, have been omitted from the list.

It will be observed that the list contains only a few minute shells. Doubtless these exist, and will be found when carefully sought for, but, as previously indicated, the majority of collectors seem to have confined their attention to the more conspicuous species.

I have included a certain number of pelagic forms, cephalopods, pteropods and nudibranchs, which are not strictly littoral, but are found occasionally thrown on the beaches or are captured within a short distance of the shore.

In any first census of this kind, some species will be included which later investigation will exclude. I have rejected a number of Tschudi's species as obviously exotic, but a small number remain which are doubtful, and which are indicated as needing confirmation. I have also omitted a few names which seemed to be almost certainly due to misidentification or to a confusion between such

localities as Arica and Africa. "Lumping" closely related species, such as some of the Siphonarias, has led certain authors to include purely Atlantic forms with their Pacific analogues under one name. So far as time, and the access to specimens, permitted I have tried to disentangle such cases and use only the name definitely belonging to the Pacific form. In making her dredgings the U. S. Fish Commission steamer *Albatross* seems to have avoided shallow water; and in the case of Dentalium, which has a wide range in depth, I have included a few species actually dredged beyond the 100 fathom line, but which will in all probability be found within it when sought for. No other deep-water species, however, has been admitted. An account of them will be found in my *Albatross* Report of 1908. In scanning the list those unfamiliar with the repetition of names so prevalent in Spanish geographical nomenclature will need to remember that there is a Tumbes in Chile as well as in Peru, and be on the look out for analogous cases. Species of Auriculidæ which are exclusively littoral, although pulmonate, have been included, also the salt-water Cyrenas, my aim being to include all species which are to be found along the shores of the province on the beaches and in the adjacent waters of the sea. Whatever deductions from the list may be necessary hereafter, I am convinced that they will be more than made up for by future additions from the ranks of the minuter species.

It is probable, though not by any means certain, that when we eliminate the overflow from the Panamic and Magellanic Provinces, the remaining fauna on this long stretch of coast may be susceptible of division into subfaunas, but it is too early to speculate about this possible feature of the distribution.

I have indicated in the preceding remark, the nature of the reservations which must be made in discussing the statistics of our present census of the Peruvian Fauna, and subject to those reservations we may now proceed to consider the figures.

The total number of species appears to be 869, of which 64 are pelagic and may be omitted from consideration in the matter of distribution, leaving 805. Taking the present political limits of the two countries as a starting point, we find seventy-one species reported from Peru exclusively, and one hundred and three restricted to Chile. But, as political and biologic boundaries rarely have anything in common, these data are not especially significant. We have 174 species restricted to Peru or Chile and 141 common to Peru and Chile, making 315 species proper to the Province itself. In addition to these we have 253 species common to the Panamic Province and to Peru, and 239 species of the Panamic Province which are known to reach the northern border of the Peruvian Province at or near Cape Blanco, many of which will doubtless be found to have a more extended southerly range. In addition to these there are 25 species whose range extends from Upper California south to Peru or even to Valparaiso.

At the southern extreme of the Peruvian Province it receives 41 recruits from the Magellanic Province, few of which range north of Valparaiso. Of the whole 805 species enumerated which are not pelagic, only 24 are known from the West Indies or Atlantic Ocean, most of which are Pholads, borers, or limpets; forms peculiarly liable to transportation long distances on ships or floating timber. The only species which can be regarded as also Indo-Pacific, are even fewer in number and to be included in the same category.

Eliminating all the pelagic species and all the Panamic species not shown to be now actually domiciled within the limits of the Peruvian Province, we have a population for and province of 566 species of littoral marine mollusks.

In Bulletin 84, of the U. S. Geological Survey, pages 25–28, 1892, I have shown that the average population for a warm temperate area (when the temperature ranges from 60° to 70° F.) is about 500 species of shell-bearing mollusks. Adding the species of nudibranchs, naked

tectibranchs and littoral cephalopods enumerated in our list, it would seem that the average is pretty well maintained in the case of the Peruvian Province.

Dismissing the minuter species from consideration as insufficiently known, the more striking characteristics of the Peruvian fauna may be summed up as follows:

1. There is an unusual proportion of the species which are black or blackish or of a lurid tint. This feature of the fauna has attracted attention from all who have studied it, and has been discussed by von Martens. It is particularly marked among the zoophagous groups.

2. The fauna is notable for its Fissurellidæ and Acmæidæ, its trochids of the genus Tegula, its numerous and peculiar chitons, its numerous cancellarias, the development of Calyptræidæ, of species of Arcidæ and of Thais, Chione, Semele, Petricola, Mulinia, all represented by numerous species.

3. The deficiencies in the fauna are as marked as the redundancies. There are notably few pectens or Lucinas, and the Tellinidæ are poorly represented. Acteon, the smaller tectibranchs, Conus, the Turritidæ especially, the Marginellidæ, Fusinus and its allies, Epitonium (Scala) and the Pyramidellidæ are all very poorly represented. Calliostoma and Margarita, Haliotis and Pleurotomaria are absent or barely represented.

The notion that the mournful colors of so many of the species might be correlated with the huge beds of kelp characteristic of these shores, seems to be negatived by the fact that in California similar kelp-beds afford a shelter to some of the most brightly colored Trochidæ, etc., and that, as I am informed by Mr. Coker, red and green seaweeds are abundant on the rocks below low-water mark, on a large part of the coast of Peru, and presumably also of Chile. This and a number of other problems await the investigators of the future.

Lastly, a survey of the characteristic groups of which the fauna is largely made up leads to the conclusion that the fauna is chiefly of southern origin. In spite of the

fact that many species are common to the Panamic fauna and a relatively small number to the Magellanic fauna, the more conspicuous types, like the blackish species of Tegula, have a Magellanic rather than a tropical character. This particular group has extended its range to Alaska on the north, and Japan on the northwest, but its metropolis is in southern Chile. The type represented by the various species of Thais and Acanthina has traveled the same road, and so has the Protothaca group of Veneridæ.

If we may accept as the original metropolis of a special type of mollusk that region where it is developed in the greatest number and variety of species and perhaps also with the most extreme limits of size and ornamentation, we shall have for example Buccinum and Chrysodomus focused in the boreal Pacific region; certain types of Thais and Acanthina in the region of southern Chile. Cook has called attention to the relation between *Thais lapillus* and the Oregonian *T. lamellosa,* and other species in the tropics of the Panamic and Antiliean region; but viewed from an eastern Pacific standpoint the relatively few Atlantic forms may easily have originated in the Pacific where their existing representatives show a much more luxuriant development. There is only one Thais of the nucella type in the north Atlantic, but the north Pacific has five or six. It is very remarkable that in the Peruvian Province we have not a single distinctively old-world type of Mollusk. Those which seem to be such are really cosmopolitan types more familiar to us from old-world localities, perhaps, but not necessarily of old-world origin.

REMARKABLE DEVELOPMENT OF STARFISHES ON THE NORTHWEST AMERICAN COAST; HYBRIDISM; MULTIPLICITY OF RAYS; TERATOLOGY; PROBLEMS IN EVOLUTION; GEOGRAPHICAL DISTRIBUTION

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No other part of the world, of similar extent, so far as known, has so many species of shallow water and littoral starfishes as the coasts of Alaska and British Columbia, including Puget Sound. Many of the species range from San Francisco to the Aleutian Islands, but the most favored region is from Puget Sound to southern Alaska.

The forms known to me, including those from arctic Alaska, are about eighty species, besides fifteen named varieties. No doubt special physical conditions there have favored the remarkable development of this group, as well as certain other groups, on that coast.[1]

The entire region has a very broken coast line, innumerable islands, bays, fiords and straits, giving a great extent of sheltered coast line, bathed in pure sea-water and swept by strong tidal currents, all of which are very favorable to littoral marine life, vegetable as well as animal, thus providing an abundance of food for carnivorous forms, like the starfishes, most of which feed principally on mollusks.

These favorable conditions are notably shown by the great abundance of individuals as well as species, and also by the great size that many of the species attain. At least eight of the species of Asterias and allies become there over two feet in diameter.[2]

[1] Among other groups having a similar remarkable development on that coast are the Polyplacophora (Chitons), limpets, nemerteans, tubicolous annelids (Sabellidæ), etc.

[2] Among these very large species are *Asterias columbiana* Ver., *A. Troschelii* (St.) var. *rudis* V., *A. forcipulata* Ver., *Pisaster ochraceus* (Br.),

Perhaps the relative uniformity of the temperature during the entire year is one of the most important factors in determining, or permitting, the great abundance of life on this coast, just as it is in the deep sea. Although the water is cold, it is not subject to great extremes of heat and cold, like those of the eastern coast of North America. The rapid tidal currents have a powerful effect in preventing extremes of temperature, by constantly mixing the deeper water with the shallow.

But the nature of the starfish fauna and that of other groups, like the chitons, forces us to conclude that similar favorable conditions have existed on that coast continuously for several geological periods, and that no great extermination of marine life occurred there, even during the glacial period.

A number of the genera and higher groups are peculiar to that coast; others have there a remarkable development in number and variety of species, showing that their evolution must have gone along continuously for vast periods of time. In many cases primitive and highly specialized species of a family are associated. Therefore, that coast offers unusually favorable conditions for studying the evolution of the genera and species, having there their chief development. We should naturally expect to find still surviving there, representatives of some of the comparatively early or primitive species, associated with those of more modern origin, of the same groups. Such appears to be the actual condition in many instances.

However, the complete elucidation of these questions will require a large amount of careful investigation and very extensive collections.[3]

P. giganteus (St.), *P. Lutkeni* (St.), *P. papulosus* Ver., *Pycnopodia helianthoides* St. Also *Asterias acanthostoma* sp. nov., allied to *Troschelii*, but with long proximal adambulacral spines; dorsal spines small, acute, reticulated; proximally in transverse combs; rays very long.

[3] The collections that I have personally studied are large, but not always as complete as desirable. They are from the Canada Geological Survey, the Provincial Museum of British Columbia, Washington State University, Yale University Museum, U. S. National Museum, Harriman Alaska Expedition and others.

Hybridism

One difficulty in these studies arises from the fact that certain of the species, usually very distinct, seem to hybridize in localities where their ranges overlap and the breeding seasons are coincident. Owing to the small variations in temperature the breeding season of most species is probably unusually prolonged, and this affords better opportunities for hybridization. Among such apparent hybrids, I will mention particularly those between *Asterias epichlora,* a small, usually six-rayed, diplacanthid species, and *Pisaster ochraceus* (fig. 7), a large, coarse, five-rayed, monacanthid species. The latter ranges from San Diego, Cal., to middle Alaska, and is one of the most abundant littoral species. The former ranges from Puget Sound to the Aleutian Islands. At Sitka and adjacent regions, on rocky shores, it is one of the very abundant littoral species. Although normally six-rayed, five-rayed specimens are common. It is one of those species that have the habit of carrying the eggs and young attached in clusters around the mouth.

From Sitka, Wrangel, etc., I have had a considerable number of specimens that appear to be true hybrids between these two very diverse species. They generally have the small size and form of *epichlora,* but some have the reticulated and nodular arrangement of the dorsal spines of *ochraceus.* And what is still more striking, several of them, looking like true *epichlora,* have more or less of the huge, sessile, dentate, dermal pedicellariæ (fig. 7) characteristic of *ochraceus* and the other species of Pisaster.

I have named six marked varieties of *epichlora,* which do not seem to depend on hybridization; or at least I could not satisfy myself of it. But those that I consider hybrids do not conform to any of the determinate varieties. However, it is easy to understand that if hybrids occur, as I believe they do, between *A. epichlora* and *A. hexactis,* which are much more closely allied and also occur commonly together, it would not be easy to determine the

fact. The same would be true in the case of hybrids between either of the latter and *A. Troschelii,* another commonly associated species at Sitka, etc. For although the latter is a large, five-rayed species, with long rays, when young it often closely resembles some varieties of *epichlora.* Therefore it is not very unlikely that some of the so-called varieties of the latter may also be hybrids. More extensive collections with minute comparisons can alone determine such questions.

The number of species of starfishes on that coast of the family Asteriidæ (usually referred to the genus Asterias), known to me is forty, with twelve named varieties. With so many species, many of them with overlapping ranges, numerous hybrids are likely to occur. The same remarks would, most likely, apply to certain groups of mollusks, annelids, etc., in which large numbers of species occur together.

Multiplicity of Rays

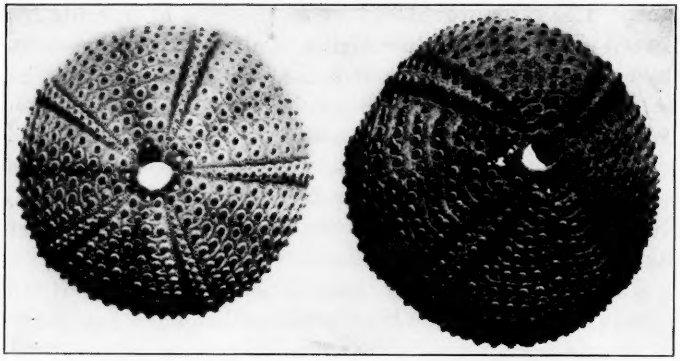
So far as known to me, no other region can be compared with the northwest coast, in respect to multiplicity of rays. It is particularly noticeable in the Asteriidæ, a family that is generally five-rayed in all other parts of the world, though there are many exceptions.[4]

On the northeast coast of America there are only two exceptions: *Asterias polaris,* with six rays (Labrador and northward), and *Stephanasterias albula,* with six to nine rays, and autotomous; (from New England northward). Of the forty northwest American species of Asterias and Pisaster, twelve, or thirty per cent., have normally six rays.[5]

Besides these, the remarkable related genus, *Pycnopodia,* is peculiar to that coast. Its single species, *P. heli-*

[4] It is also noteworthy that the genus Heliaster with several species, having from twenty-four to fifty or more rays, is peculiar to the Pacific coast of America (Lower California to Peru). The record of one species from Hawaiian waters is probably an error.

[5] Among these are *Pisaster giganteus* (St.), *A. polythela* Ver., *A. hexactis* (St.), *A. æqualis* (St.), *A. epichlora* (Br.), *A. polaris* var. *acervata* (St.), *A. macropora* Ver., *A. Katherinæ* Gray, *A. dubia* Ver. = *A. Katherinæ* Per., *non* Gray.



a b
FIG. 1.—*Arbacia æquituberculata; a*, normal form; *b*, quadriradial specimen.

anthoides, which ranges from California to middle Alaska (Yakutat, etc.), has, when adult, twenty to twenty-four rays. It begins life as a five-rayed or six-rayed star, but acquires new rays, by budding in new rays, a pair at a time, symmetrically and side by side in succession.[6] This process is not known to occur in any other starfish, except in Labidiaster, which is an Antarctic genus of the family Brisingidæ. Several peculiar Antarctic starfishes seem to be allied to north Pacific forms.

But even those species of Asterias, etc., that are ordinarily five-rayed, occur not very rarely with six rays,[7] and the six-rayed species may occur with five rays (see note, teratology). In other families the same peculiarity is

[6] See Professor W. E. Ritter and G. R. Crocker (*Proc. Washington Acad. Sci.*, Vol. II, pp. 247–274, 1900), who give a good account of the process. I have observed many examples like theirs, but have also studied some in which there were five primary rays, and a few in which some new rays were produced, also, at irregular places, but this is unusual.

[7] I have recently collected many specimens of the very common five rayed New England species, *A. Forbesii*, near New Haven, Conn., which have four rays and six rays, and some that have seven, eight and even nine rays, by examining many thousands. About 1 in 2,000 has six rays; 1 in about 3,000 is four-rayed; 1 in about 10,000 is seven- or eight-rayed, at this time and place. Some of those with more than six rays may be due to complete repairs of injuries received in early life, with development of extra rays. (See H. I. King, "Regeneration in *Asterias vulgaris*," *Arch. Entwickel. Organ.*, IX, pp. 724–730, 1900). But this is evidently not the case with most of the four-rayed and six-rayed instances.

noticeable. Thus the peculiar genus Pteraster, which carries its young in a dorsal marsupial pouch, is found all around the world, rather sparingly, and with one exception[8] all the known species have until now, been five-rayed. The very young, taken from the pouch, agree in number of rays with the mother. On the northwest coast six shallow-water species are known, besides an additional allied genus.[9] One of these (*P. octaster* Ver.) has eight rays; another six rays.

Of Solaster, five shallow-water species are known. Of these, one (*S. constellatus* Ver.) seems to have, normally, but eight rays, an unusual number in the genus. The others have from nine to thirteen rays, the number varying in each species.

Teratology

Besides the species that normally have an increased number of rays, or vary indefinitely, there are others which have, more or less rarely, a smaller or larger number, as monstrosities. I propose to mention here a few such cases. Various other monstrous variations occur somewhat frequently, such as forked rays, supernumerary rays arising from the dorsal surface, etc. But these will mostly be discussed elsewhere.

The common large *Asterina miniata,* which ranges from south of San Francisco, Cal., to middle Alaska, becomes 175 mm. in diameter. It is normally five-rayed, but I have studied more than a dozen six-rayed specimens (fig. 2), which are regular and normal in all other respects; some are of full size; most of the large six-rayed ones were collected at Ocean Grove, Ore., by Professor W. R. Coe. In the same lot was one four-rayed specimen, 135 mm. in diameter. It is a little irregular, the greater part of one ray having been reproduced, but not to full size.

[8] *Pteraster* (*Hexaster*), *obscurus* (Per.) = *Temnaster hexactis* Ver., has normally six rays (rarely seven). It is from Newfoundland Banks and Arctic ocean. Two other shallow water species occur on the New England coast, both five-rayed.

[9] This genus *Pterasterides* Ver. nov. is proposed for *P. aporus* Ludwig. It is peculiar in having no dorsal osculum and in having spines around the central nephridial pore that do not reach the marsupial dorsal membrane.

Dermasterias imbricata is a common five-rayed or pentagonal species, but we have one regular, six-rayed, young specimen from Sitka. The majority of our specimens have numerous large bivalve and trivalve pedicellariæ in rows, below, and smaller ones dorsally, though most writers describe it as destitute of pedicellariæ. A regular six-rayed *Henricia læviuscula* from Alaska occurred, and also a six-rayed *H. sanguinolenta* var. *pectinata* from Bering Sea.

Solaster Stimpsoni Ver. = *Crossaster vancouverensis* De Loriol, 1897. One specimen of this species from British Columbia has one of the rays forked below, near the mouth, thus producing ten regular rays as seen from

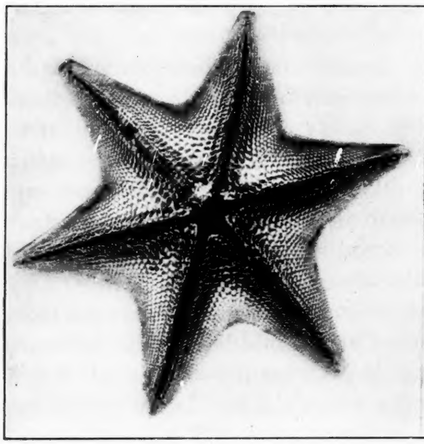


FIG. 2. FIG. 3.

FIG. 2.—*Asterina miniata;* 6-rayed example, reduced.

FIG. 3.—*Ctenodiscus cristatus;* *a*, normal, underside; *b*, 4-rayed.

above; the forking affects the ambulacral groove and jaw, the corresponding jaw being nearly abortive. The number of rays varies from nine to eleven.

Pisaster ochraceus (Br.). One medium-sized specimen from Monterey and a large one from British Columbia have six regular rays.

Asterias (*Leptasterias*) *hexactis* (St.). Several five-rayed specimens from Sitka agree with the typical six-

rayed ones in size and structural details. One from Vancouver Island has seven regular rays.

Asterias epichlora (Brandt). Although this species was originally described as five-rayed, its normal, or most common condition is six-rayed (var. *alaskensis* Ver., var. nov.), with a more or less evident median dorsal row of small capitate spines, and numerous smaller capitate spines forming a reticulated pattern over the back.[10] One specimen from Victoria has seven rays, due to the forking of one ray about at the middle; another is regularly eight-rayed. The five-rayed form is, perhaps, rather too frequent to be classified under Teratology, but in the several collections of *epichlora* examined by me, at least 90 per cent. of the specimens were six-rayed. The young, carried by six-rayed adults, were all six-rayed.

Ctenodiscus crispatus. Of this abundant species I have from New England a considerable number of regular four-rayed specimens. The few west coast specimens are five-rayed (fig. 3, *a*, *b*).

Significance of Radial Variation; a Problem in Evolution

When we consider the geological antiquity and remarkable persistence of the five-rayed condition[11] in echinoderms, generally, it seems remarkable that so many genera and species of existing starfishes should have acquired the peculiarity of having higher numbers.

All the classes of echinoderms, except perhaps holothurians, had attained highly organized and specialized conditions even in the Ordivician period. With the exception of certain cystidians and a few true crinoids, the

[10] Whiteaves, De Loriol (1897) and others have incorrectly identified *A. Troschelii* as this species. The five-rayed form is apparently the same as *A. saänichensis* De Loriol, described and figured in 1897, *Mem. Soc. Phys. Geneva*, Vol. XXXII, No. IX, p. 23, pl. ii (xvii), figs. 3–5.

[11] The case is analogous to that of gastropods, which in primordial times acquired the habit of forming right-handed spiral shells, which has prevailed through all the geological ages, though there are some modern families and genera that are normally left-handed, and some species that are as often left-handed as right-handed (Achatinella sp.). No good reason is known why the left-handed condition is not as good as the other.

numerous known Silurian species of crinoids, starfishes, ophiurans and echinoids were regularly five-rayed.

From the Devonian, several genera of starfishes with multiple rays are known. They have the aspect of Crossaster, Labidiaster and Cronaster. But their real affinities are doubtful. Those tound in the Mesozoic and Tertiary times, with rare exceptions, are five-rayed.

At the present time all echinoids and holothurians are normally five-rayed. Instances of monstrous specimens with four rays or six rays are very rare in these large and universally distributed groups.[12]

The modern crinoids only rarely depart from the five-rayed condition, even as monstrosities. The ophiurans show more variation in this respect. The common genus Ophiactis, varies, when young, from six-rayed to eight-rayed in nearly all of its species. But such species are usually autotomous, and when adult become regularly either five-rayed or six-rayed.

Ophiocoma pumila, at Bermuda, is about as often regularly six-rayed as five-rayed. *Ophioglypha hexactis* of Kerguelen Island is regularly six-rayed.

I have observed a large, regular, four-rayed example of *Ophiomusium Lymani* from deep water off the New England coast, but it was selected from thousands of five-rayed ones. Other radial variations in ophiurans are known to me, but they are not common, although the species are very numerous and many are often taken in vast numbers.

Among living starfishes radial variations are far more

[12] In the Museum of Yale University there is a full grown, regularly four-rayed example of the sea-urchin, *Arbacia æquituberculata* (Fig. 1, *b*), from the Azores. So far as known to me this is the only known instance in that common species.

Bell (*Jour. Linn. Soc. London,* Vol. XV, p. 126, pl. v, 1880) described a quadriradiate specimen of a sea-urchin, *Amblypneustes formosa,* but it was not quite regularly developed.

Stewart, *op. cit.,* p. 130, described a specimen of *A. griseus* with six ambulacra, but that, also, was somewhat irregularly developed.

Philippi (*Arch. für Naturg.,* 1837, III, p. 241, pl. v) described a quadriradiate *Echinus melo,* which was also a little irregular. A few other cases are known among echinoids.

common than in either of the other classes, as already indicated. But why this is so is a perplexing problem in evolution.

No doubt there are some advantages in the five-rayed condition, or else it would not have remained so constant through all the geologic ages. But it is equally certain that it is more advantageous for certain starfishes, in their special environments, to have six or more rays, otherwise they would not have retained this condition. We must conclude that all these variations originated, at first, as "sports," which have persisted by heredity and natural selection, because they were advantageous. It is easy to conjecture that, in the case of two starfishes, similar in size and structure, living together on a rocky shore and exposed to violent surf, the one with six rays would be able to cling more securely to the rocks than the one with five rays. Therefore, because of the increased number of ambulacral sucker-feet it might well be the form preserved by natural selection, unless for some other important but unknown reason, the five-rayed condition has certain other more important advantages.

It is certainly true that most of the species with multiple rays live among rocks in situations exposed to the surf.[13] This is true of the various shallow water and littoral species of Solaster and Crossaster, which usually have nine to thirteen rays (rarely eight or less). It is also true of the several species of Heliaster with very numerous rays, and many other such species, as well as the numerous five-rayed and six-rayed species of Asterias and Pisaster.

But the power of effectually clinging to rocks may be perfected in other ways, involving an increased number of sucker-feet. This is often attained by lengthening the rays, as in many species of Asterias; by crowding the suckers into more than four rows, as in Pycnopodia and some large species of Pisaster; and by increasing the size and strength of the suckers.

[13] The family Brisingidæ, however, is confined to deep water. All the species are multirayed, with long rays.

These same adaptations would also be useful in enabling the creatures to securely hold their prey, especially while, at the same time, holding fast to the rocks.

I am inclined to believe that the increase of rays has been due more to the advantages gained in holding the food securely than for holding to the rocks, though both go together. The starfishes are the most predacious of the echinoderms. Although they feed largely on gastropods and bivalve mollusks, they also feed on each other, and on large holothurians, echini, and other relatively large creatures.

However, we must admit that, so far as now known, the five-rayed and six-rayed individuals of a species appear to be equally well nourished and grow to equal size. Also that the normally six-rayed species of Asterias are no larger, nor more robust, than the allied five-rayed species, in the same environment. Even the four-rayed individuals, including the four-rayed sea-urchin (Arbacia), mentioned above, appear to be well fed and of average size.

Some, at least, of the many-rayed Brisingidæ use their slender rays for clinging to the deep-sea Gorgonians. I have observed that the *Odinia americana* Ver. thus clings to the branches of *Paragorgia arborea* with its twenty long rays. In such cases numerous rays would be advantageous.

It must be borne in mind that the variation in the number of rays is necessarily attended by extensive changes in the number, size and form of all the skeletal plates; also in the number of ambulacral feet and water tubes, nerve ganglions, nerve cords, stomach lobes, hepatic glands and all other internal organs. A six-rayed specimen has twelve reproductive glands, instead of the ten in its five-rayed competitor. If the number of ovules be proportionately large, it would produce twenty per cent. more young. So, likewise, it would have an additional stomach-lobe and two more hepatic glands. This would, perhaps, be of considerable advantage in the digestion of food and cause more rapid growth. We know that

there is great variation in the size of different individuals of young starfishes of equal age, of the same species, dependent on temperature and relative abundance of food. But I know of no experiments or observations to connect this with the number of congenital rays.

Distribution

A number of Arctic species occur in Bering Sea and as far south as the Aleutian Islands, or somewhat farther. Most of these are circumpolar, as *Crossaster papposus, Solaster endeca, Henricia sanguinolenta, Ctenodiscus crispatus, Asterias polaris, Asterias hyperborea* (=*A. arctica Murd.*), *A. grœnlandica*=*A. cribraria* St. and others.

Some Arctic species are peculiar to the north Pacific side, so far as known, as *Pterasterides aporus* (Ludwig), *Tosia arctica* Ver., *Asterias polythela* Ver., *Allasterias rathbuni* Verrill, *Pteraster octaster* Ver.[14] and others.

But exclusive of the Arctic forms, the entire starfish fauna of the coast, from the Aleutian Islands to San Francisco, is peculiar to that coast, so far as I can determine, and is rather sharply limited, both northward and southward by temperatures only. Some species[15] are closely related to North Atlantic ones, and evidently represent divergent groups derived from a common stock, at no very remote period. However, the cases of greatest interest are those of generic types peculiar to the fauna, some of which have no near allies elsewhere. Among such genera I may mention here a few examples: *Pyconopodia,* with no near allies; *Acantharchaster* Ver., a very isolated genus; *Dermasterias,* with a single species; *Glyphaster* Ver. (type *Leptychaster anomalus* Fisher), with

[14] These last four species are described in the *Amer. Jour. Science,* July, 1909, with others from the same coast.

[15] Among these are *Hippasteria spinosa* Ver., closely related to *H. phrygiana; Leptychaster millespina* Ver., closely related to *L. arctica.* It differs in having smaller dorsal paxilli with fewer spinules, more transversely elongated supero-marginal plates; much finer and more numerous adambulacral spines, four or five in the furrow series. *Mediaster æqualis* St., related to *M. bairdii* V.; *Luidia foliata* Gr., allied to *L. clathrata.* Some of these were evidently derived from Arctic forms.

FIG. 7.

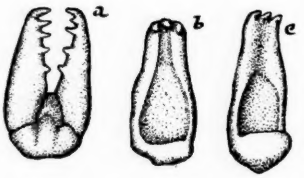
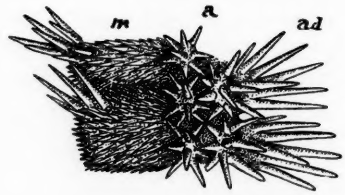


FIG. 4.



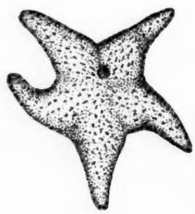


FIG. 5.

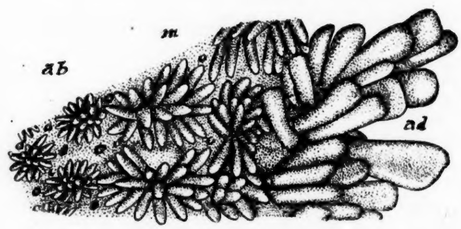


FIG. 6.

FIG. 4.—*Bunodaster Ritteri* nov.; *ad*, adambulacral spines; actinals; *m*, marginals.

FIG. 5.—*Henricia tumida* Ver. sp. nov.

FIG. 6.—*H. spatulifera* sp. nov.; *ad*, adambulacral spines; *m*, marginals; *ab*, abactinal pseudopaxillæ; much enlarged.

FIG. 7.—Large unguiculate and denticulate dorsal pedicellariæ of *Pisaster ochraceus; b, c,* separated valves.

one species (*G. anomalus*): and especially *Pisaster,* which has there eight, large, massive species (mentioned above, p. 542). I am unable to refer with certainty any of the species described as *Asterias,* from other regions, to this group, as restricted, unless it be the six-rayed species, *A. Perrieri* Smith,[16] from Kerguelen I. This agrees with it closely. It is monacanthid and has large dentate pedicellariæ.

Cosmasterias sulcifera (Per.) Sla., from southern South America, is also pretty nearly allied to Pisaster, but is diplacanthid and has few dorsal major pedicellariæ, which are not particularly large. This is the type of Cosmasterias Sla. and it seems better to keep the latter name for this and allied diplacanthid species. It is evident, however, that these Antarctic forms are the nearest relatives of Pisaster.

Bunodaster, gen. nov., resembles Astropecten, but has

[16] *Trans. Phil. Soc.*, Vol. 168, p. 273, pl. xvi, figs. 2–2*b*, 1879.

convex abactinal *pseudopaxillæ;* triangular actinal area of about three V-shaped rows of tesselated plates; curtailed inferomarginals; numerous adambulacral spines. Type *B. Ritteri,* nov. (Fig. 4), has inferomarginals with a distal group of small spines, elsewhere finely spinulose; furrow spines about five to a plate and eight to twelve on actinal side; no spines on superomarginals. California (Prof. W. G. Ritter).

The peculiar northern species, *Allasterias rathbuni,* is represented on the Asiatic coast by *A. versicolor* (Sla. sp. of Japan), which has alternately one and two ambulacral spines, and by *A. amurensis* (Lutk.), Japan to Siberia. Many of the other species of Asteriidæ are only remotely allied to those known in other faunæ. This family and the genus Asterias are world-wide in distribution, but no other region has such a variety of forms.

The family Pterasteridæ is also uncommonly well developed. Seven species have been found in shallow water, besides others in deep water. They all belong to the restricted genus Pteraster, except the remarkable form, *P. aporus* Ludwig, for which I have proposed the new genus Pterasterides (see p. 547, note). It has no dorsal osculum, and the spines around the nephridial or central pore do not reach the marsupial membrane. The Retaster, described by Clark from Puget Sound, I refer to Pteraster (*P. gracilis*). The *P. reticulatus* Ives, which ranges from Puget Sound to middle Alaska, is a very large species and is the most common one. *P. hebes* Ver. and *P. octaster* Ver. are very unlike any species from other regions.

The genus Henricia (formerly Cribrella) is also represented by numerous species and varieties. *H. tumida* Ver., from North Alaska, Cape Fox and C. Disburne, Fig. 1, is remarkable for its large swollen disk and short, stout rays. *H. spatulifera* Ver. southeast Alaska, Fig. 2, is remarkable for its broad paddle-shaped or spatuliform adambulacral spines which are much crowded proximally (see figures).

SHORTER ARTICLES AND CORRESPONDENCE

IS THERE A SELECTIVE ELIMINATION OF OVARIES IN THE FRUITING OF THE LEGUMINOSÆ?

During the past few years I have had occasion to have counted the number of ovules formed per pod in series of many thousands of pods of various species of Leguminosæ. While engaged at this work a side problem of considerable interest presented itself. Since time to follow this up has not been forthcoming for a couple of years, I will publish my data and suggestions for the benefit of any unoccupied botanist.

It is evident that the distribution of ovules, as seen in series of mature pods, does not necessarily represent that of the ovules in the newly formed ovaries. It is possible that the distribution of ovules per ovary in the flower buds may have been modified as the fruits matured by a selective elimination of certain classes of pods. This selective elimination might modify mean or variability or both. One such case is very probably to be found in ovaries with but a single ovule in species normally producing several. If the single ovule be fertilized it may develop into a seed or not, according to various circumstances; but if it fail to develop, the pod will, in most cases at least, fall from the plant. Whether the same factor is at work in the case of ovule classes of a higher order can only be determined by special investigation, but it seems quite possible that such an influence might affect very materially the constants of mature as compared with newly formed ovaries.

In the spring of 1907 I attempted to get some light on this question by the collection of material at different times from individual red bud trees, *Cercis Canadensis*, growing in the North American Tract of the Missouri Botanical Garden.

The flowers of Cercis are produced in an umbel-like cluster from the old wood. These clusters are composed of from two to seventeen flowers. Many of the inflorescences produce only one to four fruits. The per cent. of flowers which mature fruits varies widely from year to year and from tree to tree, but it is evident that there is a very heavy elimination of ovaries. The question to be answered is: Have the eliminated ovaries a dif-

ferent mean or variability, or both, for the number of ovules which they produce than those which develop into mature fruits?

Cercis seems to be a form well adapted to an investigation of this question. The ovaries can be quickly dissected out of the flowers which have been dropped into alcohol for preservation. Absolute alcohol renders the walls sufficiently clear that by the aid of the light from a properly adjusted mirror of the dissecting microscope the ovules may be counted very easily. Clove oil may be used as a clearing agent, but it soon renders the ovules as well as the walls transparent, and great watchfulness is required in the countings.

On March 28 a series of one hundred inflorescences was taken from each of three trees and dropped into alcohol for future study. This was at a time when most of the flowers were open, but when none had fallen from the trees. The whole inflorescence was taken because (*a*) it was desirable to avoid any possibility of an unconscious selection of flowers in gathering, and (*b*) because it seemed desirable to determine whether the position of an ovary on the inflorescence might exert any influence upon the number of ovules produced.

On April 3 a second lot of material was collected, but in an entirely different manner. Many of the blossoms were ready to fall. The trees were shaken, not too violently, so as to secure the flowers which were ready to drop, but not to dislodge those with ovaries which might continue to develop. In preserving this material all the flowers belonging to inflorescences which had fallen were discarded, since it seemed possible that some of them might have been brushed off by twigs rubbing together. All the flowers were open, and, if their very frayed condition may be taken as a criterion, most of them had been visited by insects. The ovaries were dissected out of the flowers at once and dropped into absolute alcohol. Unfortunately the second collection from Tree II was lost.

On April 6 a third collection was made in the same manner as the second.

My intention had been to collect the matured pods of these trees in the fall for comparison with the ovaries taken in earlier stages of development, but, unfortunately, the severe frosts which followed the early opening of spring in St. Louis, in 1907, killed most of the Cercis fruits and precluded the carrying out of this part of the work.

In taking up the counting of the ovules per pod it was found that the alcohol had rendered the material so brittle that it was out of the question to keep the flowers in serial order from the base of the inflorescence, and consequently all attempt at a determination of this point was abandoned for the first collection. As a matter of fact the flowers are so closely grouped in the inflorescence of the red bud that the determination of their sequence would not be easy even in freshly gathered clusters. *A priori,* one would suppose that in an inflorescence so shortened as this, position on the axis would have little influence upon the character of the ovaries. But of course this point should be investigated, for if there is a sensible correlation between position on the inflorescence axis and number of ovules, and between the position of an ovary on the inflorescence and its chances of growing into a mature fruit, this might introduce a serious difficulty into the comparison of eliminated and matured ovaries, in consequence of those of certain types being eliminated merely because of their position on the inflorescence.

TABLE I

FREQUENCY OF NUMBERS OF OVULES PER OVARY IN VARIOUS COLLECTIONS OF CERCIS

Tree.	0	1	2	3	4	5	6	7	8	9	10	?	Totals.
I.—Lot 1					3	1	49	279	476	76	4	11	899
I.—Lot 2				2	1	2	8	113	219	39	3	4	391
I.—Lot 3						1	28	113	179	32	3	2	358
II.—Lot 1	1	1	5	32	177	327	431	100	4			10	1088
II.—Lot 3				2	58	126	112	21	2			1	322
III.—Lot 1			10	23	198	341	179	11				14	776
III.—Lot 2			4	8	85	177	63	5				1	343
III.—Lot 3			2	10	81	170	77	6	1			1	348

The numbers of ovules per ovary for the several series of material are seriated in Table I. In a very small percentage of the cases it was impossible for one reason or another to determine the number of ovules. These cases are placed in the ? column; in calculations they have not been considered, N being reduced by their number. I have no reason to think that these ovaries are in any way different from the others, and so they might have been discarded without comment, but in material of this kind it is best to account for every individual. Perhaps the single entry in the 0 column is due to one of the ovaries being too young.

The constants from Table I are given in Table II.

Regarding first the means, we note that there is no constant difference between those of the different collections. This is true without considering the probable errors, which at once take away any opportunity for theorizing on these points. Inspection shows the same conclusion to be necessary concerning both absolute and relative variabilities.

TABLE II

CONSTANTS FOR OVULES PER OVARY IN VARIOUS COLLECTIONS OF CERCIS

Collections.	Total Ovaries.	Mean and Probable Error.	Standard Deviation and Probable Error.	Coefficient of Variation.
Tree I. Lot 1	888	7.6531±.0172	.7631±.0122	9.9718
Tree I. Lot 2	387	7.7312±.0276	.8070±.0195	10.4386
Tree I. Lot 3	356	7.6235±.0285	.7995±.0202	10.4875
Tree II. Lot 1	1077	5.3556±.0207	1.0091±.0146	18.8429
Tree II. Lot 3	321	5.3052±.0331	.8826±.0234	16.6375
Tree III. Lot 1	762	4.9041±.0216	.8844±.0152	18.0339
Tree III. Lot 2	342	4.8830±.0299	.8224±.0212	16.8426
Tree III. Lot 3	347	4.9567±.0306	.8459±.0236	17.0677

So far as this series of data goes, therefore, we have no reason to think there is any selection in the elimination of the ovaries which do not develop into mature fruits. Most unfortunately the mature fruits are not available for comparison. This renders it necessary to draw the comparisons not between the constants for all the ovaries formed and the fruits maturing, but between the constants for the original population of ovaries and those for the fallen flowers. While not so satisfactory as the former method, the latter is quite justified in the present case, since the second collection represented the first of the ovaries to be eliminated from the tree and the third was taken from the main bulk of those which were to fall. During the last two years I have not succeeded in getting suitable data for the number of the ovules in trustworthy samples of ovaries formed and ovaries maturing in either this or other species of Leguminosæ. In our present dearth of quantitative data concerning selective elimination, this seems a good line to follow far enough to get conclusive positive or negative results. Perhaps some other botanist can collect adequate masses of data.

J. ARTHUR HARRIS.

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NOTES AND LITERATURE

ICHTHYOLOGY

Ichthyological Notes.—The State Laboratory of Natural History of Illinois has published an elaborate work entitled "The Fishes of Illinois," by Dr. Stephen A. Forbes and Robert Earl Richardson. In this work is given a full account of the topography of the state of Illinois, with excellent descriptions of all the species of fishes found in the state. Many of these are illustrated by colored plates, and the work is done with admirable conscientiousness and accuracy. An especial feature of the work is the very full account of the food of the different species of fishes.

In the *Proceedings of the United States National Museum* (Vol. XXXV, 1908), Professor J. O. Snyder describes eighteen new species of fishes from southern Japan and from the Riu Kiu Islands. Professor Snyder was the first ichthyologist to visit this most interesting group of islands.

In the same *Proceedings,* Professor Theodore Gill shows that the name Chœrodon is the oldest name for the genus commonly called Chœrops.

In the same *Proceedings,* Professor Snyder describes two rare fishes, from California, *Rimicola eigenmanni,* with which *R. muscarum* is identical, and *Plagiogrammus hopkinsi.*

In the *Proceedings of the Academy of Natural Sciences of Philadelphia* (1908), Henry W. Fowler gives an excellent synopsis of the Cyprinidæ of Pennsylvania, with notes on the material examined by Professor Cope. One new species, *Notropis keimi,* is described from the Allegheny River.

In "Annales de la Société Géologique du Nord" (T. XXXVI, 1907), Maurice Lariche presents observations on the fossil fishes of Patagonia, showing that the species of shark recently described as Cretaceous belong to the lower Miocene.

In the same *Proceedings* (T. XXXV, 1906), Lariche gives a review of the fossil fishes of the north of France. In his nomenclature he pays little attention to the law of priority.

In the same *Proceedings,* Lariche records various fossils from Brittany and other parts of France.

In the *Bulletin of the Geological Society of Belgium* (1908), Lariche records the presence of a species of Amia in the Hampstead Beds of the Isle of Wight.

In "Comptes rendus de l'Association Française pour l'Avancement des Sciences," Congress of Lyons (1906), Lariche describes and figures numerous species from Tertiary rocks near Montpellier.

The same author describes, in the "Annales de l'Université de Lyon" (1908), the vertebrates of the Nummulitique de l'Aude.

In the *Bulletin of the Museum of Natural History,* of Paris (1908), Dr. Jacques Pellegrin describes numerous characins from South America.

In "La Revue Coloniale" of Paris (1908), Dr. Pellegrin discusses the fresh water fishes of French Guiana, with their vernacular names.

In the *Bulletin of the Southern California Academy of Sciences* (1909), Mr. J. Z. Gilbert publishes an account of certain California flounders, with a figure of an unnamed fossil flounder from Miocene rocks at Lompoc, California. This species belongs to the large-mouthed group, with very strong teeth, but the body cavity is considerably larger than in the related species of the present time. The species will soon be described in detail by Mr. Gilbert.

In the *Proceedings of the Academy of Natural Sciences of Philadelphia* (1908), Professor Snyder describes the large ribbon-fish from Monterey Bay, California, under the name of *Trachypterus seleniris.*

In the *Proceedings of the New York State Teachers Association* for 1907, Dr. Wilder discusses the usefulness of the dogfish for educational purposes.

In the *Proceedings of the American Philosophical Society* for 1908, Dr. Wilder discusses the brain of the extraordinary Japanese Chimæra, *Rhinochimæra pacifica.* Dr. Wilder looks forward to the time when "no child shall reach the age of ten without exposing for himself, drawing, describing and dissecting the brain of some shark."

In the *Popular Science Monthly* (October, 1908), Professor W. S. Tower describes "The Passing of the Sturgeon" in America, the five species being practically exterminated all at once by murderous fishing methods. The most aggravated case

of this kind is the destruction of the species inhabiting the Lake of the Woods by Michigan fishermen who took them by thousands from their spawning beds in Rainy River, preserving the eggs for caviar and throwing the bodies away.

In the *Biological Bulletin,* XIV (1908), B. G. Smith records the spawning habits of the minnow Chrosomus, this work being part of a series of investigations undertaken by the advanced students of Professor Jacob Reighard, of the University of Michigan.

In the *Bulletin of the Bureau of Fisheries* (Vol. XXVII, 1907), Professor Snyder records the "Fishes of the Coastal Streams of California," *Hybopsis crameri, Rhinichthys evermanni* and *Ptychocheilus umpquæ* are described as new species from the Umpqua region in Oregon, and *Catostomus humboldtianus* from Humboldt County, California. Professor Snyder shows that *Leuciscus caurinus* is a species of Leuciscus, and not identical with *Mylocheilus lateralis.* Professor Snyder gives an interesting map of the coastwise streams, showing the distribution of the different faunal groups.

In the same *Bulletin,* Professor Snyder discusses the "Fish Fauna of the Lakes of Southeastern Oregon" with reference to the distribution of the different forms. *Catostomus warnerensis* and *Rutilus oregonensis* from Warner Lake, and *Rutilus columbianus* from the Columbia River, are described as new species. A map of the isolated Warner Lake region, the remains of Lake Idaho, is given.

In the same *Bulletin,* the paper on the habits and distribution. of fishes in the Sacramento Basin, by the late Cloudsley Rutter, is published. The manuscript, prepared before the death of the lamented author, who was one of the most careful observers of fishes connected with the Bureau of Fisheries, has been revised by Dr. Evermann. In this paper, *Catostomus microps, Cottus asperrima*(*us*) and *Cottus macrops,* new species from Modoc County, California, are described.

In the same *Bulletin* (1908), Jordan and Richardson describe the fishes collected in the Philippines by Richard Crittenden McGregor. Eleven new species are described and figured, and two hundred and ninety-five species are mentioned with critical notes.

In the *Hamburger Magalhæensische Sammelreise* (1907), Pro-

fessor Einar Lönnberg describes the species taken in the Straits of Magellan.

In the Publications of the Department of Education of Ontario (1908), Mr. C. W. Nash, of Toronto, publishes a catalogue of the fishes of Ontario, with plates of many of the more important species. This is prepared primarily for the use of the teachers of Ontario, and is part of a volume containing all the vertebrate animals. It will prove extremely useful for the purposes for which it was prepared.

In a report of the Biological Survey of State of Michigan (1907), Thomas L. Hankinson gives a biological survey of Walnut Lake, with numerous plates, photographs and other illustrations, showing the nature of the fauna and flora.

In the Michigan Academy of Science, Mr. Hankinson gives a list of fishes of Hillsdale County, Michigan.

In the *Annuaire du Musée Zoologique de l'Académie Impériale des Science de St. Pétersbourg* (T. XIII, 1908), L. Berg gives a list of the fishes of the River Kolyma, with descriptions, mostly in Russian, of the various species found there.

In the same *Annuaire* is given a list of the fishes of the River Obi.

In the *Journal of the College of Sciences of the Imperial University of Tokyo* (1908), Shigeho Tanaka describes six new species and two new genera of fishes from Japan, with notes on other rare forms.

In the *Annotations Zoologicæ Japonenses* (1908), Tanaka gives a description of eight additional new species from Japan.

In the same *Journal* (1908), Tanaka describes "Tide-Pool Fishes of Misaki, Japan," with two additional new species.

In the same *Journal,* Tanaka records the fishes of Lake Biwa, with one new species.

In the *Zoological Magazine* (1908), Tanaka again records, in Japanese, the fishes of Lake Biwa, the largest of the Japanese lakes.

In the *Transactions of the Natural History Society of Sapporo,* Professor K. Otaki describes the Stickle-backs of Japan, in Japanese and in English, one new species being described.

In the same *Transactions,* Professor Otaki describes the common sturgeon of northern Japan, *Acipenser mikadoi.*

In the *Sitzungsberichten of the Vienna Academy* (1908), Dr.

Viktor Pietschmann describes the sharks of Japan, with descriptions of some new species.

In the same *Sitzungsberichten,* Dr. Pietschmann describes also two new Japanese species of shark, and he has also a paper comparing the European species of *Mustelus* with each other.

In the Smithsonian Miscellaneous Collections (1908), Professor Gill gives in detail the story of the devilfish, Manta, with numerous illustrative plates.

In the *Proceedings of the Zoological Society of London* (1908), Dr. Regan gives a valuable revision of the sharks of the family Orectolobidæ. To this family he refers Rhinodon, Ginglymostoma and other forms usually placed in separate families.

In the *Annals and Magazine of Natural History* (1908), Mr. Regan describes a collection of fresh-water fishes from Costa Rica, with several new species. *Joturus stipes,* from Central America, is made the type of a new genus, Xenorhynchichthys. A new genus, Tomocichla, near Herichthys, is also described.

In the same *Annals,* Mr. Regan discusses the systematic position of Stylophorus, which he places near the Allotriognathi. He discusses the work of Professor Starks on the same species, who, in the *Bulletin of the Museum of Comparative Zoology,* for 1908, makes Stylophorus the type of a new suborder, Atelaxia. The work of both of these anatomists shows that Stylophorus is related to Trachypterus and also to Velifer.

In the same *Annals,* Mr. Regan revises the species and subspecies of Coregonus found in Great Britain.

In the same *Annals,* Mr. Regan revises the char of Great Britain, adding a number of new species. Four old species and five new ones are recognized in place of the single *Salvelinus alpinus,* recognized by Day as found in British waters.

In the same *Annals,* Mr. Regan describes the species of char, six in number, found in the rivers of Ireland. He recognizes the fact that these species are of relatively recent date, and perhaps only partially separated from one another.

In the same *Annals,* Mr. Regan discusses a classification of the scombroid fishes, or mackerel-like fishes. He recognizes the extremely close relation of the Carangidæ with the perch-like forms, or Serranidæ.

In the same *Annals,* Mr. Regan revises the genus Elops, showing that instead of a single species, *Elops saurus,* there are seven well-marked species. This conclusion the writer has been

able to verify in part, having specimens of *Elops hawaiensis* from Formosa as well as from Hawaii. Regan describes *Elops affinis,* from Mazatlan and Jalisco, the species being based on a specimen sent as *Elops saurus* by the present writer.

In the same *Annals* (1909), Mr. Regan takes up the impossible problem of defining the orders and sub-orders and equivalent groups of the teleostean or bony fishes. The paper is most suggestive and valuable, but no one adjustment of the intricate interrelationships of these fishes is likely to be more permanent than any other. It is encouraging, however, to notice the practical agreement between Mr. Regan's classifications and those adopted by American naturalists in matters in which the facts have become clearly apprehended.

In the same *Annals,* Mr. Regan gives an account of the fishes of the group Salanginæ, mostly of eastern Asia.

In the same *Annals,* Mr. Regan gives an account of new fishes from Lake Candidius, in Formosa.

In the *Annals of the South African Museum* (1908), J. D. F. Gilchrist and W. W. Thompson give descriptions of fishes from the coast of Natal, with descriptions of numerous species.

In the same *Annals,* Gilchrist and Thompson give an account of the blennies of South Africa, the species referred to Clinus being especially numerous.

In the *Annals of the Queensland Museum,* J. D. Ogilby describes numerous new or little-known fishes from the Queensland Museum in Brisbane. Among other things, he claims that the name Dampieria should supersede Labracinus, recently resurrected to take the place of Cichlops, which is preoccupied.

In the Publications of the Department of Fisheries for New South Wales, David G. Stead gives an interesting account of the beaked salmon, Gonorhynchus.

In the same Publications Mr. Stead gives descriptions of three new species of fishes from New South Wales.

In the *Proceedings of the Royal Society of Queensland* (1907), Mr. J. D. Ogilby describes seven new species of fishes from the coast of Queensland. He divides the genus Tylosurus into three, separating from it Stenocaulus, with body short and deep, the type being *krefftii,* and Eurycaulus, with the caudal peduncle strongly keeled, the type *platyura.*

In the same *Proceedings,* Mr. Ogilby describes numerous new species and genera of fishes from Queensland.

In the "Scientific Investigations of the Fishes of Ireland" (No. V, 1908), Holt and Byrne record certain fishes of the Irish Atlantic Slope.

In the *Bulletin of the Department of Agriculture in the Dutch East Indies* (1908), Van Kampen describes the larva of Megalops, which passes through changes similar to those already recorded for Albula.

In the Norwegian journal *Naturen* for 1908, Stejneger discusses in Norwegian the species of char found in Norway, *Salvelinus salvelinus* and *Salvelinus alpinus.*

In the *Journal of Comparative Neurology and Psychology* (Vol. XVIII, No. 6, 1908), Professor J. B. Johnston describes in detail the nervous system of the lamprey.

In the same *Journal,* Professor Johnston further discusses the physiology of the nerves of the lamprey.

In the *Anatomical Record* (Vol. II, No. 6, 1908), Professor Johnston discusses the question of the presence of the glossopharyngeal nerve in the hagfish.

In the same *Journal,* Professor Stockard gives a note on the same subject.

In the *Zoologischen Jahrbuchern of Jiessen* (1908), E. P. Allis, Jr., discusses the bloodvessels in various bony fishes.

In the same *Journal,* Dr. E. Philippi discusses the name and development of certain viviparous fishes of the genus Glaridichthys.

In the American Breeders Association (Vol. IV), the Committee on Breeding Fish, J. W. Titcomb, Chairman, discuss the possibility of improvement of fish stock by selective breeding.

In the *Memoirs of the Royal Society of Copenhagen* (1908), Dr. H. F. E. Jungersen gives an elaborate account of the genera of fishes related to Centriscus. This is a most valuable contribution to our knowledge of the fishes of this type, and ought to help settle the questions as to their relationship to other related forms.

In the *Transactions of the Royal Society of Edinburgh* (Vol. 45, 1907), W. E. Agar gives a valuable account of the paired fins in Lepidosiren and Protopterus, with special reference to the nerve structures.

In the Annual Report of the Department of Marine and Fisheries for Canada, are given valuable studies of the effect of dynamite explosions and sawdust on fish life. The evil effects

of dynamite are here clearly emphasized by Professor A. P. Knight. Professor Knight does not, however, find the effect of sawdust as injurious as has been hitherto supposed. A strong solution of sawdust poisons fish and fish fry, through the agency of compounds dissolved out of the wood cells. Fishes will desert a river polluted with freshly made sawdust, going down stream or into tributaries to escape from the disagreeable influence of the sawdust extracts. Waste matters which would be deadly in one river will pass away and prove of little harm in another, where the conditions are different.

In the *Journal of Morphology* (1908), Reighard and Mast describe the development of the hypophysis of Amia.

In the *Journal of Experimental Zoology* (1909), Professor C. R. Stockard describes the development of the young of *Fundulus heteroclitus* in magnesian solutions instead of salt water. The result is the development of cyclopean fish, with a single coalesced eye on the top of the head. It is thought that magnesia possesses an anesthetic effect, and is inhibitory in its influence on muscular activity. It, therefore, retards the outpushing of the eyes in the embryo, leaving the eyes without energy for perfect development, and at times without energy sufficient for their normal separation.

In the *Outing Magazine* (September, 1908), Bonnycastle Dale describes the mystery of the salmon, and its desperate struggle to breed in the waters of the Columbia, with some excellent photographs.

Under the head of "The Fishes of Japan," Otaki, Fujita and Higurashi continue their fifth volume of discussion of the Japanese fisheries and fishing methods. The fourth volume contains colored plates of a number of Japanese food fishes. The text is entirely in Japanese.

DAVID STARR JORDAN.

PARASITOLOGY

The question as to the relation of the tse-tse fly which is absolutely demonstrated to be the transmitting agent of sleeping sickness and the parasite of the disease is one that has been discussed pro and con with great vigor. Minchin and others contend most powerfully that the fly is a mere mechanical vector while Manson and his supporters, chiefly, it must be confessed,

from a theoretical standpoint, have maintained that the fly stood in the same relation to the disease as the mosquito held to malaria. As already indicated, the definite evidence thus far secured has seemed to favor the view that the fly is a mere mechanical agent. Some recent experiments in East Africa are of tremendous importance in this discussion. Kleine[1] under date of December 28, 1908, reports from Kirugu, German East Africa, an experiment which apparently demonstrates that flies may infect after a long interval. Heretofore it has been claimed that flies would not infect later than forty-eight hours after biting infected hosts. A longer interval is good evidence of the existence of a developmental cycle in the fly. Kleine's experiment may be summarized as follows:

Nagana, an animal disease due to *Trypanosoma Brucei,* does not occur in the Kirugu region. Animals which had been naturally infected by the bite of the tse-tse fly, *Glossina morsitans,* were brought from a locality seven days' march distant and were kept in isolation. Other flies, *Glossina palpalis,* caught on the Mori River, were fed for three days on the infected animals and from the fourth to the seventeenth day inclusive for each day on a fresh healthy animal. From the eighteenth to the twenty-fourth day the flies fed on a single sheep; from the twenty-fifth to the twenty-ninth day on a single ox. Frequent blood examinations were made of the experimental animals and on the twelfth day after the flies were put on the ox which was first used on the twenty-fifth day of the experiment, numerous trypanosomes were found in the blood of this host. Then the sheep first employed as host on the eighteenth day was examined and found also to be infected. All the other experimental animals remained uninfected. Goats, calves and sheep were used to feed the flies from the fortieth to the fiftieth day and all were infected. The author concludes: "From this it is seen that flies which for many days after the ingestion of blood containing trypanosomes were not infective, afterwards became so and infected a sheep and then an ox."

The Royal Society has received a telegram dated April 3 from Colonel Sir David Bruce which announces the confirmation of Kleine's observations, and a letter received April 30, dated Mpumu, Chagwe, Uganda, April 3, confirms the cablegram

[1] "Positive Infektionsversuche mit *Trypanosoma Brucei* durch *Glossina palpalis.*" *Deutsche medizinische Wochenschrift,* 18 Marz, 1909; 469–470.

notice and says that the Commission had "repeated Dr. Kleine's experiments with *Trypanosoma gambiense* and *Glossina palpalis*, also with a trypanosome of the *dimorphon* type and the same tse-tse flies and found the flies infective after 16, 19 and 22 days."

It is apparently impossible to escape the conclusion that the parasite of human sleeping sickness, *Trypanosoma gambiense*, also undergoes a cycle of development in its transmitting agent, *Glossina palpalis*, and that the fly bears the same relation to the parasite which the mosquito does to the malarial organism. It is unnecessary to indicate in detail the tremendous importance of this discovery.

Old fables die hard and among them must be placed the oft-repeated story cited in many modern texts of good standing that in some parts of Italy and France the population makes use of certain fish tapeworms (Ligula) which are found in the body cavity of various cyprinids, as a delicacy under the name of macaroni piatti or ver blanc. In 1894 Monticelli demonstrated the incorrectness of the story, but it continues to be cited as a biological marvel even by recent writers of repute. Recently Parona has again exploded the myth in an interesting brochure entitled "Les Liguliphages ou soi-distant mangeurs des ligules."[1] Nowhere in Italy is such a habit found; the error is as persistent as false and deserves general contradiction until it is finally eliminated from our text-books. Rudolphi reported that at times the Ligulæ are eaten with the tench which they infest, being taken for the fat of the fish. From such a simple beginning the fable grew until it was said that certain fish culturists raised tench to obtain the ligulæ which they harbored. The final stamp of reality was imparted to the fable when a French savant wrote that these biological noodles are eaten at Lyons as in Italy!! Like the tales of early naturalists, which Linné copied so faithfully, that tapeworms occur in brooks and springs, so let the marvellous story of the liguliphages be consigned to the care of writers on unnatural history and forever more be eliminated from serious consideration.

Sambon and Seligman[2] have recorded studies on the hæmogregarine of reptiles, describing many new species and affirming

[1] *Bull. pop. pisiculture*, n. s., 4.
[2] *Jour. Trop. Med.*, December, 1908.

that their life history manifests two cycles; the schizogonic or vegetative cycle, in the blood of vertebrates and characterized by asexual multiplication with the sporogonic, characterized by sexual reproduction. They enumerate merozoites, schizonts, sporonts, etc. Patton[3] recounting his work on the same objects states that careful feeding operations with larval nymphal and adult ticks under most favorable conditions at the King Institute, Madras, and several years' study of similar parasites in amphibia and their transmitting leeches, for comparative purposes, have entirely failed to elucidate the extra-corporeal life histories of the intracellular parasites of either reptiles or mammals. He regards the transmission of these parasites as mechanical and questions the interpretation of the different forms described by the other authors from the peripheral blood of snakes. He inclines to consider all their forms as belonging to a single species of hæmogregarine and in closing calls attention to Prowazek's error in regarding cysts found in a pentastome from a python as developmental stages of *Hæmogregarina pythonis* when in reality they represent part of a cycle of a parasite peculiar to the pentastome and have nothing to do with the hæmogregarine of the snake. Patton might have cited numerous similar cases of confusion between normal parasites of a supposed transmitting agent and the missing developmental stages of the parasite under investigation.

In the same journal[4] Patton gives a brief though valuable résumé of the genus *Herpetomonas* which emphasizes certain points of great importance in this connection. These flagellates are parasitic in the alimentary tract of insects, though those which occur in blood-sucking insects are in no wise related to blood parasites. Their developmental cycle consists of a preflagellate, a flagellate and a postflagellate stage. The preflagellate stage presents round or oval bodies with nucleus and blepharoplast, multiplies by simple longifission or multiple segmentation, and occurs in the insect's mid gut. In the flagellate stage the organism forms a single flagellum and is found in both mid gut and hind gut, while the postflagellate stage is characterized by massing of the herpetomonads in the midgut and the formation of cysts which pass out in the feces. Many are undistinguishable in their preflagellate stages and a partial study

[3] *Parasitology,* December, 1908.

[4] *Parasitology,* December, 1908.

may lead to confusion of true herpetomonads with Crithidia or young trypanosomes, such as has actually occurred in more than one instance.

He closes thus:

As the life-cycles and general structure of the three human parasites are similar to those of well-known Herpetomonads, I see no reason for placing them in a distinct genus. The differences in their development, such as the formation of the flagellum, methods of division and the fact that their preflagellate stages are passed in man only justify their being regarded as specifically distinct from such species as *H. muscæ-domesticæ*, *H. sarcophagæ*, *H. culicis*, *H. lygæi* and many others.

In the opinion of others, just the points noted justify including the three human parasites in a separate genus, Leishmania.

H. B. Ward.

PLANT CYTOLOGY

The Permanence of Chromosomes in Plant Cells.—The problem of the individuality of the chromosome is receiving the attention of a number of plant cytologists. Briefly stated the problem concerns the permanence of the chromosome as an organ of the cell, enquiring whether the chromosomes are present as structural entities in the resting nucleus and whether they have come down from a line of ancestral structures reproducing by fission in the mitoses throughout the life histories.

In 1904 Rosenberg presented claims that the chromosomes may be recognized in the resting nuclei of certain plants and cited *Capsella bursa-pastoris* as a favorable type for their demonstration. Overton in 1905 traced the chromosomes of certain dicotyledons to aggregates of chromatin in the resting nuclei which he designated as prochromosomes, believing them to be autonymous structures representing the chromosomes in this stage of nuclear activity. Other investigators have reached similar conclusions. Nevertheless a number of plants is known in which the forms of the chromosomes during the interkineses are so changed by progressive alveolization or vacuolization as well as by the reticular union of chromatic masses through anastomoses that the outlines of the structures can not be followed in the irregularities of the chromatic and linin network. Whether the chromosomes in such nuclei really lose their identity as autonymous structures is not of course established simply by the negative evidence that they have not been traced

by the technical methods at our command. These difficulties, however, have been clearly set forth by Mottier and other authors, some of whom are unwilling to accept the hypothesis of the permanence of the chromosome.

Four papers have recently appeared which give further evidence of the presence of prochromosomes in the resting nucleus and also present some important conclusions on the history of the chromatin during synapsis. In the latter feature these authors (Overton, Lundegardh and Rosenberg) support the view that during synapsis the sporophytic chromosomes by the parallel association of two spirems become grouped in pairs to form the reduced number of bivalent chromosomes characteristic of the heterotypic mitosis.

Overton[1] presents the results of studies on the pollen mother-cells of *Thalictrum purpurascens, Calycanthus floridus* and *Richardia africana.* He finds that the sporophytic (somatic) nuclei previous to the heterotypic mitosis have their chromatin in the form of definite bodies arranged in pairs with linin intervals between. The bodies are prochromosomes and were traced through synapsis to the chromosomes of the heterotypic mitosis. Overton interprets the grouping of the prochromosomes in pairs to mean that there are two spirems of paternal and maternal origin in the sporophytic nuclei which he believes remain distinct throughout the sporophytic phase of the life history. The parallel threads become more distinct just before synapsis and become very closely associated during the synaptic contraction, but remain distinct from one another.

The association of the sporophytic chromosomes in pairs is most intimate during postsynaptic stages when these elements become more or less closely united in various ways to form the bivalent chromosomes (in the reduced number) characteristic of the heterotypic mitosis. This is the period in the life history when the sporophytic chromosomes are most likely to influence one another by conjugation or by the mutual interchange of substance.

The first or heterotypic mitosis in the pollen mother-cells distributes the sporophytic chromosomes associated in pairs. At this time each sporophytic chromosome undergoes a longitudinal

[1] Overton, J. B., "On the Organization of the Nuclei in the Pollen Mother-cells of Certain Plants, with Especial Reference to the Permanence of the Chromosomes," *Ann. of Bot.*, XXIII, p. 19, 1909.

fission in preparation for the second or homotypic division so that chromosome tetrads are present during the metaphase of the heterotypic mitosis. The split chromosomes remain distinct during the interkinesis between the two mitoses and the halves are distributed by the homotypic division to the nuclei of the pollen grains.

The nuclei of the pollen grains show prochromosomes arranged in a single series and it seems probable that they retain this arrangement throughout the gametophytic phase of the life history. It also seems probable that the fertilization of the egg nucleus effects the close association of two such series of chromosomes, thus accounting for the pairs of prochromosomes arranged on parallel threads, and that this association is maintained throughout the history of the sporophyte until the distribution of the sporophytic chromosomes by the heterotypic mitosis. Nevertheless it is but fair to point out that these inferences are not as yet supported by direct evidence, that is to say, the history of the chromosomes has not been followed throughout the life history of any of these seed plant.

Lundegardh[2] introduces his paper with a good summary of the two views concerning the origin of the bivalent chromosomes of the heterotypic mitosis, (1) the theory of the parallel association of two spirems (Junktionstheorie), and (2) the theory of the folding of a single spirem (Faltungstheorie). His investigations are based on several types of the *Compositæ* (*Calendula officinalis, Achillea millifolium, Anthemis tinctoria* and *Matricaria chamomilla*), and on *Trollius europæus* of the *Ranunculaceæ*. Unfortunately these forms are not treated serially but with reference to the critical phases of the processes of the reduction divisions so that it is very difficult for the reader to follow the text and figures consecutively for any of the types. The difficulty is further increased by the crowding and ill arrangement of the figures. In deference to the reader too much care can not be given to these matters.

Lundegardh finds for the types of the Compositæ that the prochromosomes (*Gamosomen*) are generally arranged in pairs (*Gamomiten*) in the resting nucleus of the pollen mother-cell. In Trollius, on the other hand, the chromatin is in the form of numerous granules distributed on a delicate linin network and

[2] Lundegardh, H., "Ueber Reduktionsteilung in den Pollenmutterzellen einiger dicotylen Pflanzen." *Svensk. Bot. Tidsk.* III, p. 78, 1909.

prochromosomes could not be recognized. As the nuclei of these Compositæ approach synapsis the pairs of prochromosomes become connected with one another by delicate threads along which the chromatic substance is distributed so that two parallel systems of threads are constructed which finally become so closely associated as to form a single spirem. The chromatin granules of Trollius gather and fuse into larger masses which are at first more numerous than the chromosome count but show a tendency to pair. These are distributed over a delicate linin network upon which the chromatin becomes distributed. Finally the chromatic masses fuse thus forming a single spirem.

The later history of the reduction processes is similar in all of the types. The spirem splits (strepsinema stage) and segments into the reduced number of bivalent chromosomes which become distributed in the nuclear cavity (diakinesis) as pairs of chromosomes. The halves of the split segments of the spirem may then be regarded as the sporophytic chromosomes to be distributed in two sets by the heterotypic mitosis. A contraction during the strepsinema stage (second contraction) is not regarded as of special significance, but merely as an accompaniment of this period in the development of the bivalent chromosomes. The phenomenon of synapsis is regarded as especially significant since it is the period when the sporophytic chromosomes are in their most intimate relation to one another.

Rosenberg in two recent papers gives additional evidence in support of his belief (1904) in the permanence of the chromosomes, and develops further his views on the significance of synaptic phenomena. The first paper[3] deals especially with *Hieracium venosum* and *H. auricula*. A brief introduction outlines clearly the problems concerned with the prochromosome or gamosome theory and their relation to the views on the interpretations of the events of synapsis and the reduction divisions.

The chromatin is present in the resting nuclei of the archesporium as irregular deeply-staining masses almost always situated at one side of the nucleus. These are interpreted to be prochromosomes or gamosomes, their number corresponding generally to the number of chromosomes which for the sporophyte is fourteen and eighteen in these two species of Hieracium. As the nuclei of the pollen mother-cells approach synapsis the prochro-

[3] Rosenberg, O., "Zur Kentniss der präsynaptischen Entwicklungsphasen der Reduktionsteilung," *Svensk Bot. Tidsk.*, I, p. 398, 1907.

mosomes are found associated in pairs distributed over a network. The further history of the reduction mitoses is not described, so that the investigation is incomplete in a number of important features.

The second paper of Rosenberg[4] deals with *Crepis virens,* one of the Compositæ, a form remarkable for the small number of chromosomes, which are six for the sporophyte and three for the gametophyte generation. A further important peculiarity is a difference in the size of the chromosomes which makes it possible to follow the individual elements through succeeding mitoses with some degree of certainty. This is, so far as the reviewer is aware, the first account for plants of such a differentiation of chromosomes as has been described for animals by a number of zoologists.

The nuclei of the sporophyte (somatic) show six small prochromosomes in the resting stage from which are organized during the prophases of the vegetative mitoses two short rod-shaped chromosomes, two very long bent elements, and two chromosomes about midway in length between these extremes. The resting nuclei of the pollen mother-cells have six prochromosomes more or less clearly grouped in pairs. Synapsis presents a series of parallel threads intimately united at intervals. From this condition a thick coiled spirem is organized which clearly shows its double nature in the frequent longitudinal separation of portions as though it were split. The free ends of the chromosomes composing the spirem may at times be distinguished. A gradual contraction of the spirem leads through stages comparable to those described as a second contraction by various authors to the period when the six chromosomes, grouped in three pairs, may be clearly recognized (diakinesis).

The chromosome group on the approach of the heterotypic mitosis consists then of a pair of small, almost spherical, chromosomes, a pair of long rods, and a pair of short rods. These correspond to the three different sizes of chromosomes present in the vegetative sporophytic mitoses, but are more condensed or shortened. Thus the heterotypic mitosis is a true reduction division distributing the six chromosomes in two sets each of which consists of a spherical chromosome, a long rod, and a chromosome intermediate in shape between these two. These

[4] Rosenberg, O., "Zur Kenntniss von den Tetradenteilungen der Compositen," *Svensk Bot. Tidsk.*, III, p. 64, 1909.

chromosomes divide during the anaphase of the heterotypic mitosis in preparation for the second or homotypic mitosis so that they appear at the poles of the heterotypic spindle in the form of three split chromosomes or pairs.

The chromosomes change their form in the interkinesis, becoming long spiral threads which shorten on the approach of the homotypic mitosis when the six chromosomes again appear as three pairs showing the same characteristic range of form. The members of these three pairs are distributed by this division so that the nucleus of each pollen grain receives three chromosomes, a short, a long, and a middle-sized element, and these may be recognized in the resting nucleus by three prochromosomes.

A brief examination of the mitoses in the embryo-sac supported the conclusions above outlined.

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